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Factors leading to the decline of European hares Lepus europaeus

Factors leading to the decline of European hares *Lepus europaeus*

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Abstract

1. European hares *Lepus europaeus* have declined throughout Europe since the 1960s, and causes are not fully understood. A review of 77 research papers from 12 European countries, and examination of temporal changes in factors associated with high and low hare numbers, indicated that habitat change caused by agricultural intensification is the ultimate cause of hare population decline. The review also highlighted the need for a better understanding of how changes in demographic processes affect population size, and for data, particularly from pastural landscapes where hare numbers are relatively low.

2. A seasonal radio-tracking study showed that heterogeneity at the within-habitat scale was more important to hares than heterogeneity at the between-habitat scale in pastural landscapes. Hares selected habitats heterogeneous in structure, selected taller vegetation during the peak breeding season, and did not select habitats based on nutritional quality. Therefore, populations in pastural landscapes are limited by habitat availability in terms of cover rather than by forage quality.

3. Population modelling, based on parameters derived from hare carcasses, a radio-tracking study and the literature, showed that population growth rates in arable and pastural landscapes were most sensitive to adult survival rates. However, recruitment limits populations in pastural landscapes as fecundity and juvenile survival rates were lower than in arable landscapes. Large increases in parameters were required to produce population growth in pastural landscapes. This suggests that it is not feasible to achieve the UK Biodiversity Action Plan target of doubling hare numbers in Britain by 2010.

4. In order to maintain and expand hare populations, agricultural management policies should focus on restoring some of the habitat heterogeneity lost through agricultural intensification, particularly in terms of structure at the within-field scale. This will create better quality forage and cover throughout the year, resulting in an increase in hare numbers and in farmland biodiversity in general.

By Nik Cole

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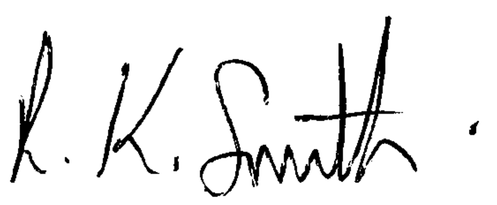
This is dedicated to Greg Avey whose

enthusiasm and courage I will never forget

Author's declaration

I declare that the work contained within this thesis was carried out in accordance with the Regulations of the University of Bristol. The work is original except where due acknowledgement has been made. No part of this thesis has been submitted for any other degree, and any views expressed in it are those of the author and in no way represent those of the University of Bristol. The thesis has not been presented to any other University for examination either in the United Kingdom or overseas.



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Abbreviations

AIMR	adjusted instantaneous mortality rate
ANCOVA	analysis of covariance
ANOVA	analysis of variance
BAP	Biodiversity Action Plan
°C	degrees centigrade
CI	confidence intervals
cm	centimetres
CV	confidence values
df	degrees of freedom
F	Fisher's test statistic
FMR	finite mortality rate
g	grammes
ha	hectares
IMR	instantaneous mortality rate
kJ	kilojoules
km	kilometres
λ	population growth rate
Λ	Wilks' lambda
ln	natural logarithm
LSU	livestock units
m	metres
MANOVA	multivariate analysis of variance
MCP	minimum convex polygon
mm	millimetres
MS	mean square
n	sample size
N_0	number of individuals alive at start time
N_t	number of individuals alive at end time
P	probability
r	Pearson correlation coefficient
r_s	Spearman's rank correlation coefficient
S	survival rates
t	time
t_0	observed time interva
t_s	standardised time interval
UK	United Kingdom
USA	United States of America
VHF	very high frequency
χ^2	chi-squared test statistic

Chapter 1

Introduction

Introduction

1.1 Population processes

The complexities of animal population dynamics have fascinated scientists for centuries. In 1798, Malthus established the modern study of the control of population growth, drawing attention to Botero's (1588) theory that animal populations increase geometrically up to the limit set by their resources. Malthus defined resources as 'room and nourishment' i.e. things an animal needs to survive and reproduce, including food, water, shelter and breeding sites. In present times, as the human population continues to grow rapidly (between 1925 and 1995 it tripled in size to almost six billion people; Primack 1995), many animal species face increasing pressure on resources. This affects animal population numbers, and many species are now in decline: in a worldwide survey of vertebrates it was found that 11% of all species of birds and mammals are threatened with extinction (Groombridge 1992; Collar, Crosby & Stattersfield 1994). Such figures show that it is now vital that we understand which factors regulate population growth, as this knowledge is fundamental to conservation management.

A population is defined as 'a group of organisms of the same species occupying a particular space at a particular time' (Krebs 1985). The fundamental characteristic of a population in which ecologists are interested is its density, i.e. population size per unit area. There are four primary population processes that affect population density: natality, mortality, immigration and emigration. Populations increase when natality and immigration outweigh mortality and emigration, and decrease when mortality and emigration outweigh natality and immigration. In order to understand why a given population starts to increase or decrease in number, we must determine which one or more of the parameters has changed, and why.

In this introduction I will begin by outlining the main factors that affect population parameters, and therefore limit population numbers. I will then focus on the effects of changes in one of these factors: resources, such as food, shelter and space.

Regulatory factors are important to populations of all species, and extensive reviews of the subject have been conducted by, among others, Krebs (1985), Sinclair (1989), Caughley & Sinclair (1994), Cappuccino & Price (1995) and Begon, Mortimer & Thompson (1996). Here I will concentrate on examples from populations of mammalian and bird species. This provides some focus for what is a vast topic, and means that examples of specific factors acting on populations are relevant to the understanding of population regulation in the study species, the European hare *Lepus europaeus*.

1.2 What are the factors that limit populations?

When conditions are favourable, animal populations tend to increase. However, numbers are kept below certain limits by the failure of the environment to satisfy their needs, by biotic factors or by physical control factors, by intra-specific competition and natural enemies or by density-dependence (Solomon 1949). Therefore populations cannot continue to increase exponentially, but are regulated by various mechanisms.

The theory of regulation in animal populations is fundamental to the understanding of population dynamics, and has been the focus of much debate by ecologists during the last century (e.g. Nicholson 1933; Andrewartha & Birch 1954; Lack 1954, 1966; Murray 1999; White 2001). The major source of debate is whether animals are regulated by density-independent factors such as climate (e.g. Andrewartha & Birch 1954) or density-dependent factors such as predation, disease and competition (e.g. Nicholson 1933; Lack 1954). It is now clear that both factors are important, and that the factors that regulate population size differ according to habitat. Species living in less favourable habitats, at the edge of their range for example, are affected more by density-independent factors (e.g. Andrewartha & Birch 1954). In contrast, populations at the centre of a species distribution, in more favourable habitats, are regulated by density-dependent factors (e.g. McCarthy 1996; Dennis & Otten 2000). Density-dependence is a negative feedback mechanism that affects population growth. When population density is below its limit, or carrying capacity in a given area, population growth rate tends to be positive and the population increases, but once population density approaches and exceeds the carrying capacity, the population growth rate slows and then stops or becomes negative, meaning that the population declines. This

happens because competition for resources increases as a population increases in size. Increased competition results in changes in the rate of mortality and natality of a population, and so reduces population numbers.

Animal populations can be regulated by either bottom-up processes, such as a shortage of a resource, or by top-down processes such as predation. Changes in any of these factors can lead to a change in population size. Andrewartha & Birch (1954) proposed that the influence of the environment on populations could be divided into four components: climate, other animals and pathogens, food, and a place in which to live. They suggested that population size depends on all four components, but that in most cases one or two of these factors are of greatest importance.

1.2.1 Climate

Early population regulation theorists proposed that climate alone regulated animal populations (e.g. Bodenheimer 1928; Uvarov 1931). This is not the case, but climate can have important effects on population size; population dynamics of both tropical and temperate ungulates are strongly influenced by climate (Sæther 1997). Climate can affect natality, mortality and dispersal within a given population, and its effects can be either direct or indirect. Direct effects include changes in metabolic costs: animals counteract heat loss caused by adverse weather conditions by increasing metabolic rate for thermoregulation. Young animals, which are unable to thermoregulate efficiently, may die of exposure. Juvenile mortality increases in Soay sheep *Ovis aries* in warm, wet and windy winters (Milner, Elston & Albon 1999), and in reindeer *Rangifer tarandus* with an increase in abundance of snow (Kumpula & Colpaert 2003). An increase in metabolic rate increases the demand for food (Nager & Noordwijk 1992), and if sufficient food is not available mortality rates increase (Redpath *et al.* 2002).

Climate also has indirect effects on population dynamics by altering food availability and abundance. In a study of sea birds, 70% of mortality occurred in winter and was linked to the effects of climate on the abundance of food (Barbraud & Weimerskirch 2003). Bird species have also been found to lay earlier in spring in response to warm temperatures, presumably due to earlier availability of food (e.g. Crick & Sparks 1999; Dunn & Winkler 1999; Sergio 2003). During years of drought, the reduction in plant biomass caused by a lack of rainfall leads to an increase in

mortality of both adult and young red kangaroos *Macropus rufus*, and decreased natality as females enter anoestrus (Newsome 1964, 1965; Cairns & Grigg 1993).

Certain climatic conditions increase the transmission rates of parasites, and so can affect population dynamics indirectly. For example, the transmission rate of the canine heartworm *Dirofilaria immitis* is driven by precipitation (Sacks, Woodward & Colwell 2003) and by temperature (Fortin & Slocombe 1981); infection with this parasite can decrease the proportion of females breeding and numbers of young produced (Nelson, Gregory & Laursen 2003).

1.2.2 Other animals: predation

Interactions between species may have positive (mutualism or commensalism) or negative (predation or competition) effects. Studies tend to concentrate on the negative interactions, and here I focus on predation in terms of the impact it has on prey populations. Competition for resources will be discussed in section *1.2.4*.

The term predation is used most frequently to mean carnivory, and this is the meaning I use here, although the term also includes herbivory, parasitism (see section *1.2.3*) and cannibalism. Predation can affect populations in two different ways, by restricting distribution or by reducing abundance due to an increase in mortality. Numerous studies have shown that the density of a prey species increases following the removal of predators from the system, including prey populations of various bird species (Côté & Sutherland 1997; Garrettson & Rohwer 2001), arctic ground squirrels *Spermophilus parryii* (Byrom *et al*. 2000), moose *Alces alces* (Gasaway *et al.* 1992) and reindeer (Seip 1992). These studies demonstrate that predators can play an important role in regulating populations. Other studies have shown that predator removal does not directly affect population density, but does affect population processes (e.g. Edminster 1939; Kauhala, Helle & Helle 2000). Predators may just be removing surplus animals that would have died for reasons such as malnutrition, disease, old age, injury or exposure (Bertram 1979; Keith *et al.* 1984; Angerbjörn 1989), in which case predation is not the main population regulator. In some systems there is a positive relationship between predator and prey numbers, as prey numbers regulate predator numbers. Decreases in numbers of coyotes *Canis latrans*, lynx *Felis lynx* and great horned owls *Bubo virginianus* lag a year behind the decline phase of a snowshoe hare *Lepus*

americanus population cycle; predator numbers increase following the increase in numbers of snowshoe hares (Keith *et al.* 1977).

The effect of predators on a population may be quite different depending on the size of the prey population. Predators may have little impact when numbers are high, but important effects on population numbers when the population is small (Angerbjörn 1989; Pech *et al.* 1992). In the case of rare prey species the presence of predators may make the difference between survival and extinction, particularly if the predator is an invasive species (e.g. Savidge 1987; Atkinson 1996; Macdonald & Harrington 2003; Nordström *et al.* 2003). Regulation by predators can also depend on populations of another prey species, for example arctic ground squirrels have lower survival rates due to predation when snowshoe hare populations are low (Byrom *et al.* 2000). This is because opportunistic predators switch between prey species depending on which species is most abundant.

1.2.3 Other animals: parasitism

Parasitism is an association between species in which one, the parasite, lives on or in the body of the other, the host. Parasites are divided into two groups: the microparasites, which include viruses, bacteria and fungi, and the macroparasites, such as arthropods e.g. fleas, and cestodes e.g. tapeworms. These parasites utilise their host as a habitat, are nutritionally dependent on the host, and cause 'harm' to their host (Anderson & May 1978). Parasites produce effects ranging from mild irritation to major diseases that lead to mortality.

Macroparasites such as fleas, lice and nematodes tend to have limited effect on hosts unless present in high numbers. For example, low numbers of feather-feeding lice have no effect on the fitness of rock doves *Columba livia* (Booth, Clayton & Block 1993). However, birds with high parasite burdens incur costs of maintaining a metabolic rate 8.5% higher because of reduced thermal protection; they lose weight and have lower over-winter survival rates than those with low burdens (Booth *et al.* 1993). Male barn swallows *Hirundo rustica* with high burdens of the chewing louse *Hirundoecus malleus* arrive at their breeding grounds later than those with low burdens (Møller, De Lope & Saino 2004). As hosts with high burdens are fairly uncommon (Anderson & Gordon 1982), these parasites have limited effects on populations.

Another example, *Trichostrongylus tenuis*, which is a gut-inhabiting nematode, has adverse effects on the body condition and natality of red grouse *Lagopus lagopus* (Potts, Tapper & Hudson 1984). The same parasite also affects mortality, as predators have been found to select red grouse with higher worm burdens, possibly due to the stronger smell of the hosts (Hudson *et al.* 1992). By affecting the average health, birth and survival rates of individuals, the parasite affects red grouse population size (Potts *et al.* 1984).

In comparison, parasites causing disease can have drastic effects on survival rates in a population. For example, when the myxoma virus was introduced to control the European rabbit *Oryctolagus cuniculus* in Australia, initial mortality rates of the population were > 95% (Fenner 1983). The mortality rate of red foxes *Vulpes vulpes* infected with rabies is 80-100% (Murray & Seward 1992). However, although parasites gain sustenance from their host and do their host harm, mortality from disease alone is rare in mammals. Death of a host only occurs if serious illness facilitates parasite transmission (e.g. in rabies), if the parasite does not depend on the host for survival, or if the parasite moves through populations over a wide area and over a long period of time (Yuill 1987). More frequently disease affects natality, normal movement or behaviour, or metabolic rates. *Brucella* species in caribou, for example, can cause females to abort their foetuses, and causes arthritis in the leg joint, making individuals more susceptible to predation (Caughley & Sinclair 1994).

1.2.4 Resources

The habitat an animal lives in contains all the resources it requires to survive; migrating animals move when suitable resources are not available in a particular area. If competition for resources increases, or the availability of resources decreases, birth and survival rates of individuals decrease (e.g. wildebeest *Connochaetes taurinus;* Mduma, Sinclair & Hilborn 1999). Resources therefore play a crucial role in the regulation of population size. In a review of the causes of mortality that regulate populations, Sinclair (1989) found that food supply regulates approximately half of the insect and bird populations studied, and almost all of the large terrestrial mammal populations. Competition for space, in the form of suitable territory or nesting sites, regulates many

small mammal populations and a third of the bird populations included in the review (Sinclair 1989).

The availability of resources can alone regulate populations, or can affect a population's ability to cope with other potentially limiting factors. If resources such as food are readily available, animals are in good physical condition, and so are more able to cope with adverse weather conditions and disease, and to evade predators (see previous sections). For example, snowshoe hares have lower winter mortality rates due to predation in food-supplemented areas than in control areas (Boutin *et al.* 1986). Similarly, if shelter is available in abundance, animals are better able to avoid the effects of adverse weather conditions, and can seek refuge from predators. Black rat *Rattus rattus* populations cope with the harsh climate on Macquarine Island by burrowing under tussock grass *Poa foliosa*; the distribution of the rats closely mirrors that of the grass (Pye, Swain & Seppelt 1999). European rabbits reach high numbers in habitats consisting of a mix of scrub and grassland, whereas abundance is limited by cover and predation in grassland, and by food availability and predation in scrubland (Lombardi *et al.* 2003). Predation on rabbits by mammalian predators is higher in grassland where rabbits are more nocturnal, and in scrub as the predators prefer cover to hunt from; predation by visually orientated birds of prey is higher in grassland (Lombardi *et al.* 2003). Changes in resources may have significant, if not devastating effects on populations.

1.3 Effects of changes in resources on population numbers

Endemic populations are adapted to cope with environmental stochasticity, including natural catastrophes such as hurricanes in some areas, which tend to cause short-term environmental changes (e.g. Pierson *et al.* 1996; Langtimm & Beck 2003; Lopez *et al.* 2003). However, long-term habitat changes, such as changes caused by humans, may influence the suitability of a habitat at levels beyond which individuals, or populations are able to respond (George & Zack 2001). Humans also cause rapid and drastic changes in habitats, which populations cannot cope with because they cannot respond quickly enough.

Recent extinction rates are at least one hundred times greater than in geological history, and habitat loss caused by humans is widely thought to be the main cause of

these extinctions (Groombridge 1992). It is the primary threat to the majority of vertebrate species currently facing extinction (Groombridge 1992). The problem is not just the complete destruction of habitats, but also the division of habitats into small fragments by roads, towns and other human developments, which isolates small populations (Primack 1995). Alternatively, habitats may remain largely intact but may be degraded by human activities such as frequent burning, pollution, changes in land use and unsustainable exploitation of particular species. Environmental pollution in the form of pesticides, industrial effluents or combustion emissions alters habitats and has devastating effects on certain populations. Toxic chemicals cause population declines by imposing an additional form of density-independent breeding failure or mortality, reducing food supply, or altering the physical or chemical structure of habitats (Sutherland 1998). For example, the contamination of habitats with organochlorine compounds such as DDT (Dichloro-diphenyl-trichloroethane), which were used as insecticides by farmers, affects natality in many bird species including the sparrowhawk *Accipiter nisus*. Seeds dressed with DDT were eaten by prey species of the sparrowhawk; natality decreased by 14 - 35% and sparrowhawk populations declined (Newton, Bogan & Rothery 1986).

Resources are also altered when land use changes. For example, when grazing of grassland by domestic animals becomes intensive, vegetation abundance and species richness changes, annual grasses and forbs dominate, and the area becomes devoid of trees and shrubs (Leggett, Fennessy & Schneider 2003). The loss of perennial grasses and browse from a habitat reduces its resistance and resilience to intensive grazing and drought (Whitford, Rapport & deSoyza 1999). During a year of drought, although water was not restricted, 90% of domestic animals and 60 - 80% of wildlife died within the Hoanib River catchment area due to competition for other resources (Viljoen 1982).

1.3.1 Agricultural intensification: implications for biodiversity

The most widespread type of land use today is agriculture, which covers 36% of the world's land area (Newman 1993). Over five thousand years of agriculture (Miller 1999) has helped to create a variety of landscapes and a rich diversity of flora and fauna. Agricultural land covers over 47% of the whole of Europe (Aebischer *et al.* 2000), and 75% of England and Wales (Grigg 1989). Therefore, changes in agricultural

landscapes affect a large proportion of Europe's biodiversity. For example, lowland farms provide habitat for almost 120 bird species that are designated Species of European Conservation Concern (globally threatened), the largest number of such species supported by any habitat in Europe (Tucker & Heath 1994; Tucker 1997). This makes the study of agricultural ecosystems and the effects of any changes in these habitats vital for wildlife conservation.

World War II and the introduction of the Common Agricultural Policy in the European Union in 1957 gave rise to an agricultural revolution that has brought about significant habitat changes throughout western Europe. Over the last 60 years farming has become increasingly intensive as farmers have focused on increasing productivity by using new more efficient farming methods and technology; agricultural intensification is defined as increased production of agricultural commodities per unit area (Donald, Green & Heath 2001). Traditional farming methods have been abandoned throughout most of western Europe; in eastern Europe food production per hectare remains lower (Donald *et al.* 2001). The change in agricultural management has brought about a huge loss of semi-natural habitat and uncropped areas of value to wildlife, including hedgerows, ancient woodland, wet grasslands and ponds (Fuller 2000). Other habitats, although they remain, have been degraded for wildlife, for example the majority of lowland grassland is now 'improved' grassland i.e. managed using fertilizers, herbicides, and sometimes reseeding, and used for intensive grazing and silage-making (Anonymous 2000; Table 1.1). The main changes in farming practices in the UK since the 1950s, and the effects these changes have had on habitats are outlined in Table 1.1; changes are likely to have been similar in other countries that were members of the European Union before 2004.

Changes in agricultural practices have affected many different aspects of the farmland habitat, but the overall result has been an increase in specialisation and synchronisation of management practices across farms and landscapes. This has lead to an increasingly homogeneous landscape, both spatially and temporally (Benton, Vickery & Wilson 2003). This is the case from the fine scale, such as within fields, to the broadest scale. In Britain agriculture has become graphically polarised: arable farming dominates in the south and east and pastural farming in the west (Figure 1.1). Since habitat heterogeneity is associated with high biodiversity, it is likely that the change to more homogeneous landscapes has played an important role in the decrease in farmland biodiversity (Benton *et al.* 2003).

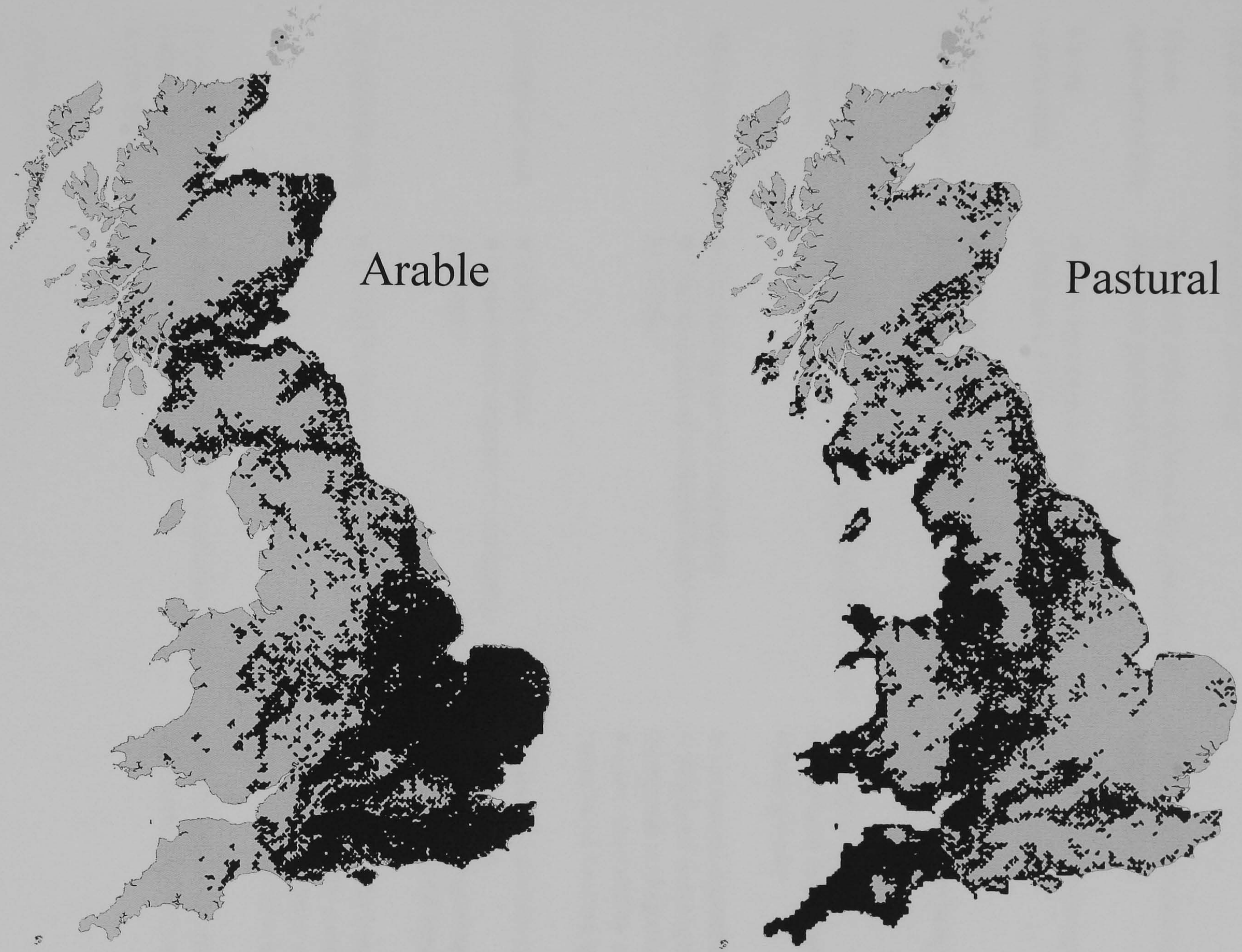

Figure. 1.1 Distribution of arable and pastural land classes (shaded black) based on the Institute of Terrestrial Ecology's land class database (now Centre for Ecology and Hydrology; adapted from Barr *et al.* 1990).

Table 1.1 Changes in farming practices in the UK since the 1950s and the effects on farmland habitats (O'Connor & Shrubb 1986; Grigg 1989; Fuller 2000; Vickery *et al.* 2001). * = botanical diversity and structural complexity.

Practice	Changes since 1950 - 60s	Effect on habitat
Mixed, arable and pastural farming		
Farm specialisation	• Mixed farms replaced by specialised arable or pastural farms	• Reduced landscape heterogeneity
Farm expansion	• 75% increase in farm size between 1960 and 1974	• Reduced landscape heterogeneity
Land conversion	• Removal of non-crop habitats e.g. ponds, small woodlands, field margins	• Habitat loss • Reduced landscape heterogeneity
Hedgerow removal	• Reduced by 25% to increase field sizes	• Habitat loss • Reduced landscape heterogeneity
Mechanization	• Escalating use of machinery • Introduction of combine harvester in 1970s	• Increased disturbance • Reduced heterogeneity (temporal and spatial) • Low availability of grain because of limited spillage
Fertiliser use	• 200% increase • Move from organic to inorganic fertilisers	• Loss of habitats e.g. leys and mixed farms • Dense fast growing crops • Reduced field heterogeneity *
Herbicide use	• *c.* 1000% increase	• Reduced field heterogeneity * • Reduction of seed-bank • Enabled autumn sowing and simplification of rotations
Pesticide use (other than herbicides)	• Increase in range, use and efficacy	• Reduced biodiversity • Presence of toxins
Arable farming		
Rotations	• Mixed systems including grass leys replaced by simple rotations using break crops such as rape and sugar beet	• Loss of habitats • Reduced farm heterogeneity
Sowing	• Autumn sowing replaced spring sowing in 1970s	• Reduction in over-winter stubbles/fallow land, and bare ground in spring • Taller denser crops in spring

Crop types	• Increase in wheat *Triticum aestivum*, rape *Brassica napus* and linseed *Linum usitatissimum* • Decrease in oats *Avena sativa*, barley *Hordeum vulgare* and potatoes *Solanum tuberosum* • Development of fast-growing, disease resistant, hardier, higher yield varieties	• Crop habitat loss/gain • Dense fast-growing crops
Yield	• Increased yields e.g. wheat 355%, sugar beet *Beta vulgaris* 46%, milk 68%, meat production 85 - 236%	• Dense fast-growing crops • Reduced field heterogeneity *
Pastural farming		
Grassland management	• Conversion to improved grassland has reduced area of unimproved grassland by 92% since 1930s • Increased use of fertilisers and anti-parasitic pesticides • Shift from hay to silage cutting in 1970s; grass is now cut up to four times per year	• Increased disturbance • Habitat loss • Reduced field * and landscape heterogeneity • Dense fast-growing grass • Reduction in seed-bank
Livestock production	• 50% increase in sheep numbers 1970 - 1990s • 18% decrease in cattle *Bos taurus* numbers (mainly dairy) • Increase in stocking density	• Increased disturbance • Reduced field heterogeneity * • Denser shorter vegetation

Humans have altered habitats throughout most of Europe's post-glacial history, but agricultural intensification has caused much greater and more widespread declines in wildlife populations than any habitat changes previously recorded (Campbell *et al.* 1997). The dramatic changes in habitats have had devastating effects on farmland biodiversity (e.g. Krebs *et al.* 1999; Benton *et al.* 2003). Population declines are best documented in bird species. Agricultural intensification has caused declines of farmland bird populations throughout Europe, and the increase in cereal yield alone caused 30% of these declines (Donald *et al.* 2001). In Britain, between 1970 and 1990, 86% of farmland bird species showed reductions in ranges, and 83% declined in abundance (Fuller *et al.* 1995). Evidence suggests that this is due to habitat changes caused by the modernisation of farm management (e.g. Krebs *et al.* 1999; Chamberlain *et al.* 2000; Vickery *et al.* 2001; Benton *et al.* 2002, 2003). Factors such as reduced availability of food e.g. invertebrates and seeds, and a reduction in nesting and

wintering sites have caused a decrease in natality and survival leading to population declines (e.g. Chamberlain *et al.* 2000; Vickery *et al.* 2001; Benton *et al.* 2002). Figure 1.2 illustrates how various changes in arable land management may have caused changes in populations of farmland insects, plants and birds. In grassland, similar changes have been caused by the intensification of grazing and grass cutting regimes (Vickery *et al.* 2001).

Declines are not only recorded in farmland birds, but in taxa such as flowering plants (Wilson 1992; Andreasen, Stryhn & Streibig 1996), arthropods (Cowley *et al.* 1999; Southerton & Self 2000), amphibians and reptiles (Cooke & Scorgie 1983) and mammals (Perrow & Jowitt 1995; Walsh & Harris 1996; Flowerdew 1997).

Data from long-term monitoring of bird abundance (Marchant *et al.* 1990) and distribution (Sharrock 1976; Gibbons, Reid & Chapman 1993) have provided evidence for the detrimental effects of agricultural intensification on bird species. The situation is very different for mammalian species. In Britain, habitat change, often caused by changes in farming, is believed to have caused declines in 31 of the 65 mammal species studied, and the use of pesticides in a further 25 species (Harris *et al.* 1995). However, there is little quantitative evidence for the effects of agricultural intensification on these populations (Robinson & Sutherland 2002). Changes in farmland management affect vegetation structure and biodiversity, invertebrates and other vertebrates (Benton *et al.* 2003), and so it is highly probable that these changes have had significant effects on many mammal populations. A study of 24 organic farms, on which agro-chemical use is very limited and rules regulate management of crops and livestock, found that the farms had higher invertebrate diversity and abundance, and higher bat activity than conventional farms (Wickramasinghe *et al.* 2003; Wickramasinghe *et al.* in press). Lesser horseshoe *Rhinolophus hipposideros* and greater horseshoe bats *Rhinolophus ferrumequinum* were only recorded on the organic farms (Wickramasinghe *et al.* 2003). In addition, wood mice *Apodemus sylvaticus* select uncultivated field margins with reduced herbicide applications over those with normal applications because of increased floral and invertebrate abundance (Tew, Macdonald & Rands 1992). The Orkney vole *Microtus arvalis orcadensis* has abandoned agricultural areas altogether during the last 50 years, and population size is now lower than in previous decades (Gorman & Reynolds 1993). These studies suggest that habitat changes caused by agricultural intensification have had significant effects on mammalian populations. Research is now required on other species to determine the mechanisms that are driving their decline.

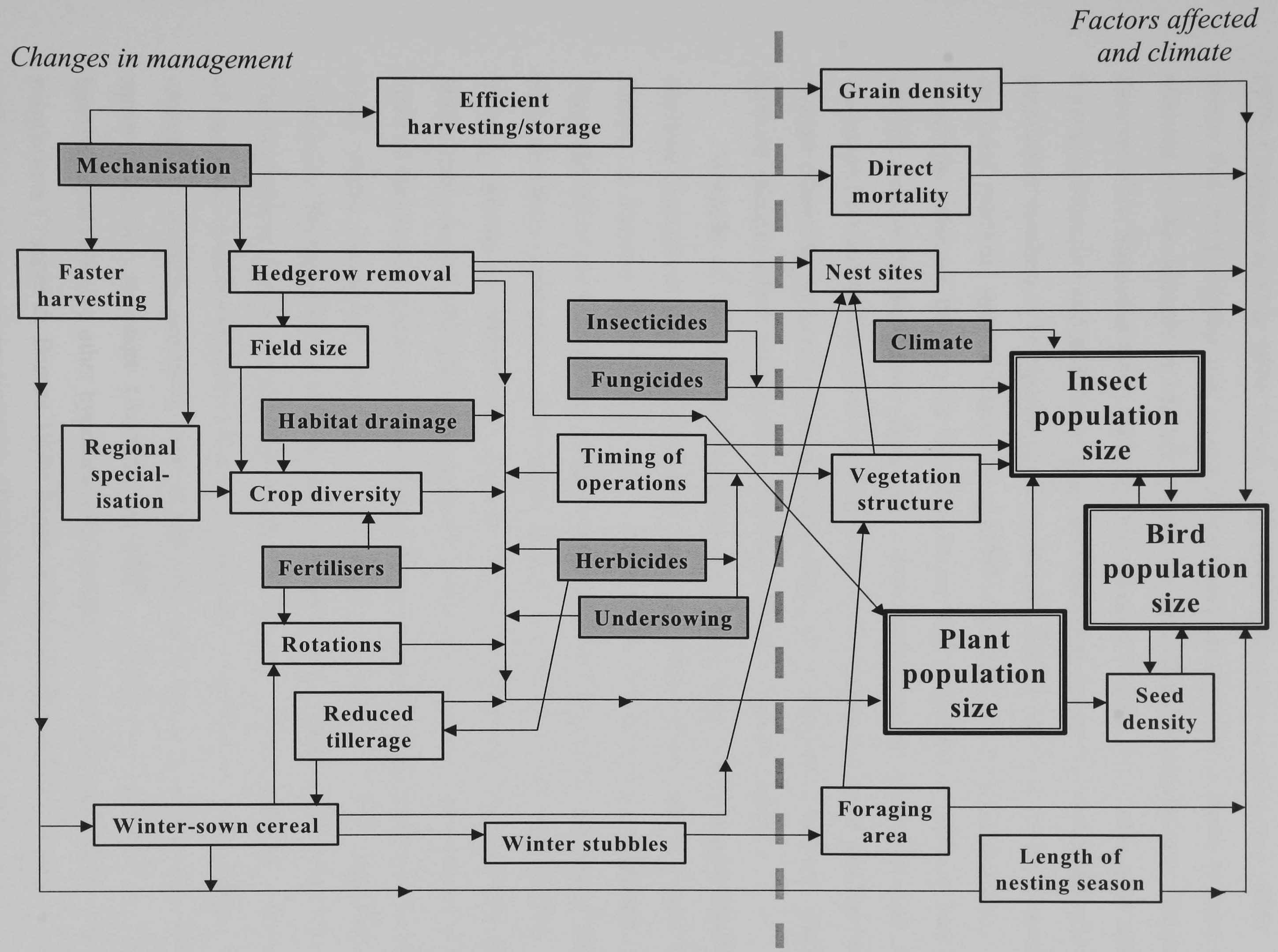

Figure 1.2 Potential causes of changes in plant, insect and bird populations caused by changes in arable management; major factors are shaded (adapted from Robinson & Sutherland 2002).

1.3.2 Agricultural intensification and the European hare

Farmland is the primary habitat of European hares throughout Europe (Meriggi & Alieri 1989; Chapman & Flux 1990; Harris *et al.* 1995; Marboutin & Aebischer 1996). This means that the European hare is one of the many species that is likely to have been affected by the changes in habitats caused by agricultural intensification (Tapper & Parsons 1984; Slamečka 1991; McLaren, Hutchings & Harris 1997). Due to its value as a game species in much of Europe, long-term data exist for the European hare allowing population numbers to be monitored. Comparable data do not exist for the majority of farmland mammal species (Harris *et al.* 1995; Robinson & Sutherland 2002). The economic value of the species has also meant that considerable research has been carried out on its population dynamics. The availability of such data makes the European hare an ideal species to study to improve our understanding of whether habitat change caused by agricultural intensification has caused population declines, and if so how the changes affect the population dynamics of a mammalian species.

Records of numbers of European hares shot suggest that populations have declined throughout Europe, particularly since the 1960s (Pielowski & Pucek 1976; Tapper & Parsons 1984; Figure 1.3). As a result, the species is protected under Appendix III of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; Anonymous 1979). In the UK it has been classed as a 'priority species of conservation concern' by the government, and therefore has a Biodiversity Action Plan (BAP; Anonymous 1995). Agricultural intensification is often cited as the primary cause of the decline of European hares, and populations are low in areas where agriculture has become very intensive (Bertoti 1975; Schröpfer and Nyenhuis 1982; Tapper and Barnes 1986; Slamečka 1991; Panek & Kamieniarz 1999). The BAP states that the main factors causing the decline in Britain are i) the conversion of grassland to arable land, ii) a loss of biodiversity in agricultural landscapes, and iii) changes in cropping practices, such as planting cereal crops in the autumn, and the move from hay to silage (Anonymous 1995). Quantitative evidence is limited, however, and there are other hypotheses for the decline, including increases in predator populations (Tapper & Barnes 1986; Panek & Kamieniarz 1999), changes in climate such as an increase in precipitation (Hackländer, Arnold & Ruf 2002a), and disease (Hutchings & Harris 1996).

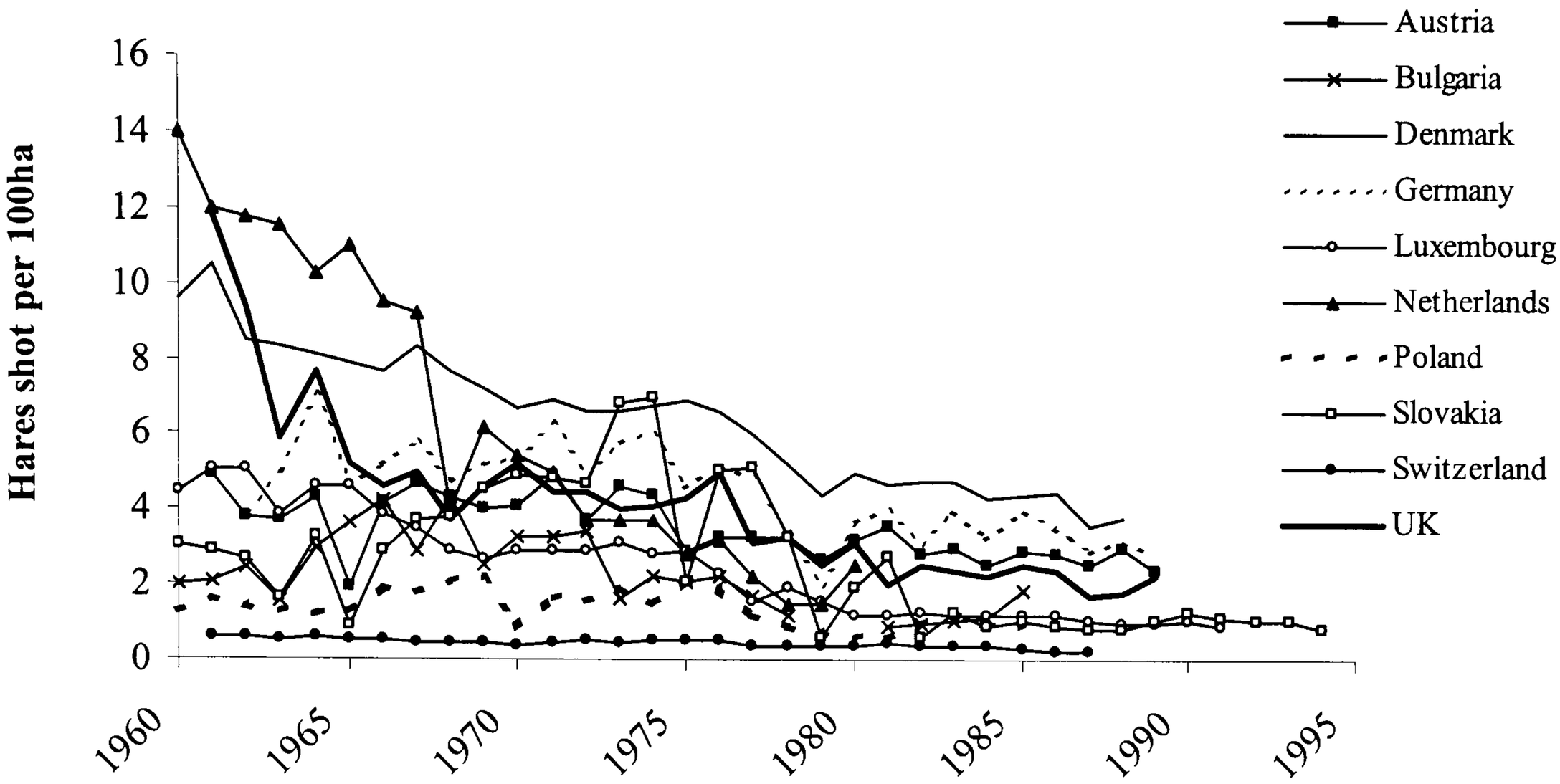

Figure 1.3 Changes in hare hunting bags (numbers shot) in Europe from 1960 onwards. Data are shown for Austria (Péroux 1995), Bulgaria (Ninov 1990), Denmark, Germany (Péroux 1995), Luxembourg (Schley *et al.* 1998), the Netherlands (Broekhuizen 1982), Poland (Pielowski 1990), Slovakia (Slamečka, Hell & Jurčík 1997), Switzerland and the UK (Péroux 1995).

Throughout its wide geographical range in Europe, the European hare is common in arable landscapes and less common in non-arable areas such as pasture, uplands and woodland (Tapper & Parsons 1984; Hutchings & Harris 1996; Klansek *et al.* 1998; Vaughan *et al.* 2003). The species evolved in open steppe, and is thought to have spread through Europe from Iran or Israel during the postglacial period, as humans turned woodland into agricultural land (Lever 1994), and to have been introduced into Britain approximately 2000 years ago (Corbet 1986). Therefore it is not understood why pastural areas support lower numbers of animals than arable areas; previous research has tended to concentrate on populations in arable landscapes. The objective of the UK European hare BAP is 'to maintain and expand existing populations, doubling spring numbers in Britain by 2010' (Anonymous 1995). Since European hares are locally common and even classed as a pest by farmers in some arable landscapes (Hutchings & Harris 1996), there is greater potential, in terms of cooperation by farmers, for management to increase numbers in pastural landscapes than in arable landscapes (McLaren *et al.* 1997). However, this requires an understanding of why pastural landscapes support low numbers of European hares, and why population

numbers have declined in recent decades. McLaren *et al.* (1997) suggest that to improve the BAP for the hare, data are needed on i) habitat use in pastural landscapes, ii) the impact of modern pastural agriculture systems on population dynamics, and in particular the importance of arable land within pastural landscapes, and iii) the degree of fragmentation and size of populations in pastural landscapes.

The aim of the work presented in this thesis is to determine which factors are most likely to have led to the decline in European hare populations, and more specifically what limits hare numbers in pastural landscapes. The latter is addressed by investigating both habitat availability and demographic parameters. The overall goal is to identify how pastural landscapes could be managed for an increase in hare numbers to achieve the objective of the BAP.

1.4 Thesis overview and conventions used

Throughout this thesis taxonomy follows Corbet & Hill (1991), Stace (1997) and Wells (1998). Geographical names follow the *Times Atlas of the World* (Times Books, London), and spelling the *Oxford English Dictionary* (Clarendon Press, Oxford). In this introductory chapter I have discussed more than one species of hare, and so have used the name 'European hare' to refer to *Lepus europaeus*; for the remainder of the thesis, I abbreviate this species to 'hare'. Other *Lepus* species discussed are referred to by their full common name. Any mention of foxes refers to the red fox *Vulpes vulpes*. Statistical analyses are carried out using SPSS for Windows (Release 10, SPSS Inc., Chicago, USA) with a significance level of 5% (Zar 1999), and averages are presented as mean ± standard deviation, unless stated otherwise.

In Chapter 2, I review published work to investigate relationships between the abundance of hares and farmland habitat characteristics throughout Europe. The effects of climate, predator numbers and hunting on abundance of hares are also investigated. I conclude that habitat change caused by agricultural intensification is the ultimate cause of declines in hare populations, and that effects of changes in climate, or predator numbers are magnified by the loss of high quality habitat. I identify a deficit of data from pastural landscapes, and a lack of knowledge as to which demographic processes have the greatest impact on population size. These issues are addressed in the next three chapters.

In Chapter 3, I describe the results of a radio-tracking study to investigate seasonal home range size and habitat selection by hares in a predominantly pastural landscape. I investigate habitat selection at two spatial scales, and conclude that heterogeneity at the within-habitat scale is more important to hares than heterogeneity at the between-habitat scale in the landscape studied. Hares tend to select habitats that are heterogeneous in structure, and avoid short homogeneous habitats. Therefore habitat availability in terms of cover may limit populations in pastural landscapes.

In Chapter 4, I describe the results of an investigation into the nutritional quality of habitats selected in each season by hares in the same pastural landscape. The aim was to identify whether hares select habitats of high nutritional quality rather than those of lower quality, and whether seasonal differences in active range size are explained by differences in forage quality. I conclude that hares do not select habitats based on nutritional quality, and that populations are not limited by habitat in terms of forage quality in pastural landscapes.

In Chapter 5, I use projection models to compare population growth rates in arable and pastural landscapes, and to identify which demographic parameters have the greatest effect on population growth. Models indicate that growth rates are most sensitive to adult survival rates. However, I conclude that recruitment (of young into the breeding population) is more likely to limit populations in pastural landscapes, and that large parameter increases are required to produce population growth in pastural landscapes.

In Chapter 6, I review the conclusions presented in this thesis on habitat availability and population dynamics of hares in pastural landscapes. I outline which population processes are causing the decline of the species, and which habitat factors are causing the changes in these parameters in agricultural landscapes. I also give recommendations for future research and conservation management for the species, and discuss the wider implications of my work.

Chapter 2

A quantitative analysis of the abundance and demography of European hares in relation to habitat type, intensity of agriculture and climate

Smith, R.K., Jennings, N.V. & Harris, S. (2005) A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Review*, **35**, in press, is based on this chapter.

A quantitative analysis of the abundance and demography of European hares in relation to habitat type, intensity of agriculture and climate

2.0 Summary

I reviewed 77 research papers in order to identify factors associated with high and low hare numbers throughout Europe. Relationships were quantified where possible. Temporal changes in factors identified as being associated with high or low numbers of hares were then examined to see if they could explain population declines. Data from pastural habitats were limited, but densities of hares were low. Arable habitats had higher densities than mixed areas in spring, unless farming was intensive, in which case densities were similar. In autumn the two habitats had similar densities. Field size, temperature, precipitation and hunting had no effect on density throughout Europe. Fecundity was affected by climate. Arable land, various crops, fallow habitat and temperature were positively associated, and monoculture, precipitation and predators negatively associated with hare abundance. The relationship of field size, pasture and woodland with abundance depended on spatial scale. Habitat changes caused by agricultural intensification are the ultimate cause of hare population declines. Effects of changes in climate or predator numbers are magnified by the loss of high quality year round forage and cover. I identified a need for further research into how habitat changes affect fecundity and survival, and to identify which parameters have the greatest impact on population numbers.

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2.1 Introduction

The intensification of agriculture results in changes such as increased mechanisation, increased agro-chemical use, and a reduction in habitat heterogeneity (see Table 1.1). Such factors are often blamed for the decline in hare numbers (e.g. Kaluzinski & Pielowski 1976; Slamečka *et al.* 1997; Edwards, Fletcher & Berny 2000), but little work has been done to quantify the effects of changes, or the relative importance of each factor on hare populations. Habitat heterogeneity is thought to be important for hares because it provides a varied diet, and year-round food and shelter (Tapper & Barnes 1986; see Chapter 3). Relationships between habitat structure, agricultural intensification, and hare populations are quantified in the literature in various ways, and at different spatial scales, and conflicting results are obtained. For example, large fields and low habitat heterogeneity are considered to be detrimental to hares (Tapper & Barnes 1986), but large fields may also be beneficial (Vaughan *et al.* 2003). The UK BAP for the hare states that the habitat needs of the species must be taken into account when reviewing or developing agri-environment schemes. This calls for a better understanding of the requirements of hares, and of how changes in habitat caused by agricultural intensification affect the species.

In this chapter, I review the published literature in order to investigate relationships between the abundance of hares and farmland habitat characteristics throughout Europe. These relationships are quantified where possible. Climate and predator numbers are also considered, as changes in these have also been used as explanations for the decline in hare numbers (e.g. predators: Tapper & Barnes 1986; Slamečka *et al.* 1997; climate: Hackländer *et al.* 2002a). The effect of hunting (killing or removing hares) on population numbers is also investigated. I i) present standardised data in summary tables, ii) quantify the effects of habitat, climate and hunting variables on the density of hares, iii) examine demographic parameters in relation to habitat and climate variables and iv) investigate the associations of hare abundance with various habitats, climate, predator numbers and hunting. By synthesising data, I identify factors associated with high and low numbers of hares throughout Europe. I then discuss temporal changes in some of these factors in relation to the decline in hare numbers

since the 1960s. The aim is to identify the main factors behind the decline of hare populations and areas in which data are lacking.

2.2 Methods

I have only included papers in which authors provided an indication of relative, estimated, or absolute density of hares and information about the habitat in the study area, or an indication of which habitats are associated with high or low abundance of hares. Papers were also included if the author provided demographic parameters along with habitat details, or gave parameters for a population for which density was estimated in a separate paper, providing data were collected at the same study site within two years. The habitat needed to be mainly farmland, the most typical habitat for this species (Meriggi & Alieri 1989; Chapman & Flux 1990; Marboutin & Aebischer 1996); information on hares in forests, saltmarshes and other unusual habitats is not included.

2.2.1 Effects of habitat, climate and hunting variables on density

Densities of hares have been assessed by clearance netting of hares driven out of known areas ('total catches', e.g. Abildgård, Andersen & Barndorff-Nielsen 1972), clearance counts of hares driven out of known areas (e.g. Pépin 1985), 'belt assessment' (counts of hares driven from strip transects, e.g. Pielowski 1969), daytime counts (e.g. Rothschild & Marsh 1956) or transect counts (e.g. Lewandowski & Nowakowski 1993), dawn or dusk counts (e.g. Frylestam 1976), and nocturnal spotlight counts (e.g. Frylestam 1979). All of these methods are considered to give good estimates of abundance (Péroux *et al.* 1998; Langbein *et al.* 1999), and so density estimates were assumed to be reliable. Daytime counts can be used to quantify the associations of hares with resting habitats, while nocturnal and crepuscular counts provide information on the use of habitats for feeding. Counts are usually carried out in spring, before the breeding season starts, or in autumn, post breeding but before winter mortality. When authors stated which season counts took place in, I assigned data accordingly, despite the fact that different

authors define spring and autumn in various ways or not at all. I defined spring as 22 March – 21 June and autumn as 24 September – 21 December, and when authors did not state the season but gave dates, I assigned data depending on when the majority of their counts took place.

Information about habitat, climate and hunting was also collected. Hunting is defined here as any deliberate human activity, which results in the removal of hares, whether for sport, food, pest control, or restocking. The effects of these variables on spring and autumn density were investigated using an analysis of covariance (ANCOVA) in which farm type (pasture, arable or mixed), intensity of farming (low, intermediate or high, as described by the author) and hunting (yes or no) were between-group factors, and climate variables (January and July temperature and annual precipitation) and field size were covariates. Only those covariates that were correlated with density (significance level of 10%) were included in the model. Variables were transformed if necessary to conform to the assumptions of ANCOVA (Zar 1999). All interaction terms were initially included in the model; non-significant interaction terms, covariates and factors were then omitted in turn and analyses repeated. Only results of the final analysis are given here.

2.2.2 Effects of habitat and climate variables on demographic parameters

The following demographic parameters were investigated in relation to type and intensity of farming, field size and climate: percentage of females breeding, numbers of leverets produced, age structure, and young and adult survival rates. Scatter plots and correlation analysis were used to investigate whether there was a relationship between the parameters and climate variables or field size. Only those that were significantly correlated are discussed here.

2.2.3 Associations with habitat, climate, predator numbers and hunting

Habitat and other variables (climate, predators and hunting) that are identified as either positively or negatively associated with abundance of hares in the studies were

summarised. Associations with abundance of hares were determined from densities, the spatial distribution of numbers of animals shot (e.g. Spittler 1976), dragline counts (e.g. Barnes, Tapper & Williams 1983), estimated relative abundance (e.g. Vaughan *et al.* 2003), or from radio-tracking (e.g. Tapper & Barnes 1986). Authors believe the variables to cause variation in density, mainly from evidence based on correlation; two studies involved habitat manipulation (Bertoti 1975; Slamečka 1991). Associations assumed by the authors, but with no data given in support, are not included.

2.3 Results

I have summarised the results of 77 original research papers published between 1952 and 2003, and covering research conducted in 12 European countries (Table 2.1). The locations of the studies are shown in Figure 2.1.

2.3.1 Effects of habitat, climate and hunting variables on density

The density of hares in pastural habitats was low (spring 9 ± 7 hares 100 hectares^{-1}, sample size, n = 6; autumn 13 ± 8 hares 100 ha^{-1}, n = 4). Due to the small number of studies carried out in pastural landscapes and in areas of low intensity farming, densities from these landscapes could not be analysed statistically ($n \leq 6$; Table 2.2). Densities for Illumø Island were not included in analyses as the population is isolated and the predator-free habitat is not typical for the species; numbers are considered higher than average for Denmark (Abildgård *et al.* 1972). The method used to estimate density had no effect on spring (Fisher's test statistic, F = 1.162, df = 4, P = 0.351) or autumn density (F = 0.702, df = 3, P = 0.558; Table 2.2).

Arable areas had significantly higher numbers of hares in spring than mixed areas (Table 2.3). However, the significant farm type*intensity interaction term showed that this was only the case in areas of intermediate intensity farming (arable 80 ± 31 hares 100 ha^{-1}, n = 3; mixed 6 ± 4 hares 100 ha^{-1}, n = 4). Where farming intensity was high there was little difference between the density of hares in arable and mixed habitats (arable 28 ± 12 hares 100 ha^{-1}, n = 16; mixed 43 ± 51 hares 100 ha^{-1}, n = 3). Precipitation and mean January temperature had no effect on spring density.

Table 2.1 Details of the studies included; ordered by country. Latitude and longitude were obtained from the Times Atlas of the World (1980); N = north; E = east; S = south; W = west; total size is of the study site or sites.

Country	Location	N latitude	E longitude	Total size (km^2)	Duration (years)	Source	Ref. No.
Austria	7 districts in the lowlands	48	16	108	1	Hackländer *et al.* (2001)	1
Bulgaria	Whole country	45	26	110912		Petrov (1976)	2
Bulgaria	Whole country	45	26	110912	44	Ninov (1990)	3
Denmark	Sjælland and Jylland	55	10		50	Andersen (1952)	4
Denmark	Illumø Island, SW coast of Fyn	55	10	1	14	Abildgård *et al.* (1972)	5
Denmark	Whole country	55	10	42930	48	Rattenborg (1991)	6
Denmark	SE of Odense on Fyn	52	10	5.3	3	Hansen (1992)	7
France	Bassin Parisien near Soissons	49	3	610	6	Pépin (1978)	8
France	Bassin Parisien near Soissons	49	3	6.5	3	Pépin (1985)	9
France	Bassin Parisien near Soissons	49	3	6.5	3	Pépin (1987)	10
France	Bassin Parisien near Soissons	49	3	6.5	3	Pépin (1989)	11
France	NW; Gatine region (Deux-Sèvres)	48	1	51.9	2	Verheyden (1991)	12
France	SW; 35km NE of Toulouse	43	1	10	2	Pépin & Cargnelutti (1994)	13
France	50km NW of Paris	49	2	20	1	Reitz & Leonard (1994)	14
France	N; Aisne	49	6	6.5	3	Marboutin & Péroux (1995)	15
France	NE	49	6	6.5	3	Marboutin & Aebischer (1996)	16
France	Central; 60 km N of Clermont-Ferrand	46	3	16.6	5	Bray (1998)	17
France	Central, Auvergne: Chareil-Montord & Chauriat	46	3		8	Marboutin *et al.* (2003)	18
Germany	Raum Euskirchen, Rheinland-Pfalz	50	8	30	10	Spittler (1976)	19

Germany	NW	51	10		11	Schropfer & Nyenhuis (1982)	20
Germany	Rheinland-Pfalz	50	8	1936	31	Mayer (1983)	21
Germany	13 regions	51	10		5	Pegel (1986)	22
Germany	W; Whole of former BDR	51	9	248890	30	Spittler (1987)	23
Germany	SW; Rheinland-Pfalz	50	8	~4002	2	Späth (1989)	24
Germany	30 hunting districts in whole country	51	10	357021	4	Petrak (1990)	25
Germany	Kleve, on Rhein NW of Düsseldorf	52	6	5	3	Spittler (1992)	26
Germany	NE; Wittow peninsular, Rügen Island	54	13	7.4	6	Ahrens *et al.* (1995)	27
Germany	8 districts in Nordrhein-Westfalen	52	9	3400	32	Nyenhuis (1995)	28
Germany	C; Thüringen	51	11		1	Nösel & Ahrens (1996)	29
Germany	E; whole of former DDR	52	13	108131	35	Schäfers (1996)	30
Germany	Nordrhein-Westfalen	52	9	2000		Spittler (1996)	31
Germany	4 regions in Saxen-Anhalt	52	12		4	Ahrens & Kotwitz (1997)	32
Germany	N	51	10	12757	2	Fehlberg (1997)	33
Germany	'Wetterau' N of Frankfurt	50	9		2	Schneider & Maar (1997)	34
Germany	Hessen region	52	10	21114	3	Eskens *et al.* (1999)	35
Germany	72 districts in NW	52	9	44000	8	Nyenhuis (1999)	36
Germany	E; Brandenburg near Berlin	52	13	12306	2	Ahrens (2000)	37
Germany	Bavaria; 305 hunting districts in 56 regions	48	12	70549	1	Kilias & Ackermann (2001)	38
Hungary	Whole country	47	19	93030	15	Szederjei (1959)	39
Hungary	On the Danube 60km W of Budapest	47	19	27.7	13	Bertoti (1975)	40
Italy	N; Pavia, Lombardia	45	9	81.2	2	Meriggi & Alieri (1989)	41
Italy	N; Padania plain, Pavia	45	9	12.2	2	Prigioni & Pelizza (1992)	42

Poland	W; Poznan province, Czempin	52	17	150	1	Raczynski (1964)	43
Poland	W; Poznan province, Czempin	52	17	201	1	Andrzejewski & Jezierski (1966)	44
Poland	10km NW of Warszawa	52	21	19	4	Pielowski (1966)	45
Poland	Poznan and Bialystok provinces	53	17	434	1	Jezierski (1968)	46
Poland	W; Poznan province, Czempin	52	17	31.5	2	Pielowski (1969)	47
Poland	W; Poznan province, Czempin	52	17	201	5	Jezierski (1973)	48
Poland	W; Poznan province, Czempin	52	17	150	9	Pielowski (1975)	49
Poland	W; Poznan province, Czempin	52	17	150	5	Bresinski (1976a)	50
Poland	W; Poznan province, Czempin	52	17	150	8	Bresinski (1976b)	51
Poland	W; Poznan province, Czempin	52	17	150	2	Bresinski & Chlewski (1976)	52
Poland	W; Poznan province, Czempin	52	17	150	9	Pielowski (1976)	53
Poland	W; Poznan province, Czempin	52	17	150	2	Bresinski (1983)	54
Poland	whole country (hunting bag); Czempin (density)	52	18	312685	29	Pielowski (1990)	55
Poland	Central; near Rogów	52	11	75	5	Wasilewski (1991)	56
Poland	E (Mazowiecka lowland) and NE (near Ketrzyn)	54	21		3	Lewandowski & Nowakowski (1993)	57
Poland	11 areas in whole country	52	19	ca.1595	14	Panek & Kamieniarz (1999)	58
Slovakia	W Slovak lowlands	48	17			Hell (1969)	59
Slovakia	Dunaj lowlands	48	17	15.6	4	Slamečka (1991)	60
Slovakia	W Slovak lowlands	48	17		9	Slamečka *et al.* (1997)	61
Slovakia, Austria	Austrian and Slovak sides of R. Morava floodplain	48	17	8.6	3	Klansek *et al.* (1998)	62
Sweden	S; Skane, Revinge, 20km E of Lund	56	13	9.5	2	Frylestam (1976)	63
Sweden	S; Skane province	56	13	4	3	Frylestam (1979)	64
Sweden	S; Skane province	56	13	6.2	3	Frylestam (1980a)	65

Sweden	S; SW of Skane province	56	13		2	Frylestam (1992)	66
Switzerland	Zürich district	47	9		49	Eiberle *et al.* (1982)	67
Switzerland	Whole county	47	8	41290	44	Eiberle (1984)	68
Switzerland	Whole country	47	8	~1090	9	Pfister (2002)	69
UK	E; Cambridgeshire, near Peterborough	53	0	8.1	3	Rothschild & Marsh (1956)	70
UK	S; NW Hampshire	51	1	7	1	Barnes *et al.* (1983)	71
UK	E England	53	1	133	3	Tapper & Barnes (1986)	72
UK	E; Suffolk	52	1	7.6	<1	Stoate & Tapper (1990)	73
UK	S; Oxfordshire	51	1	8.6	3	Bradshaw (1993)	74
UK	Whole country (not N. Ireland)	54	2	738	2	Hutchings & Harris (1996)	75
UK	S; Hampshire, Somerset, Dorset	51	2	9.0	1	Langbein *et al.* (1999)	76
UK	Whole of England and Wales	53	1	1200	1	Vaughan *et al.* (2003)	77

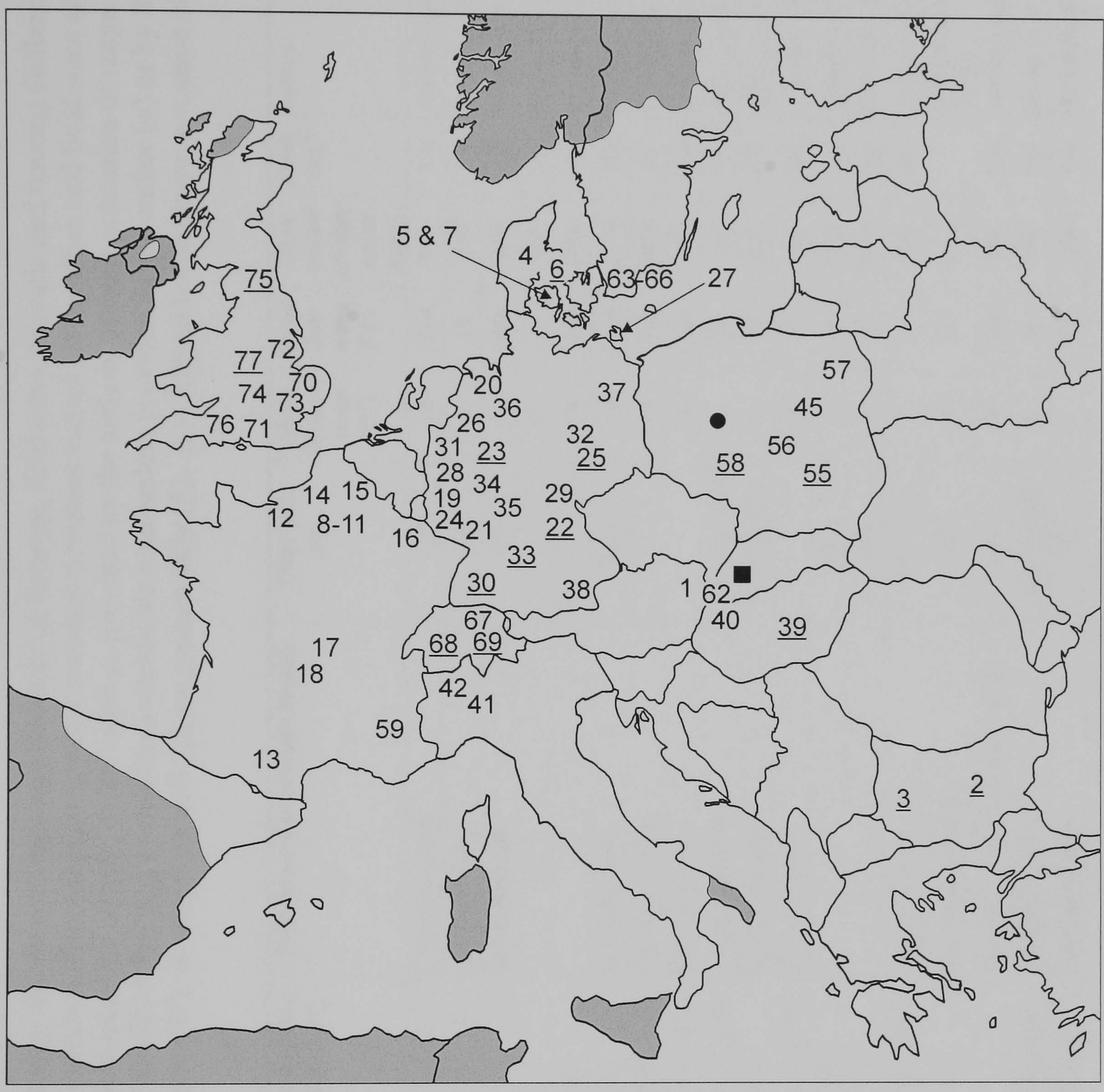

Figure 2.1 Locations of studies included. The numbers correspond to reference numbers in Table 2.1; those underlined include data from all over the country. Shaded areas represent those outside the distribution of the European hare (Corbet & Southern 1977; Mitchell-Jones *et al.* 1999). ● Poznan province, Poland, reference numbers: 6, 11, 12, 13, 14, 27, 28, 53, 54, 55, 58; ■ Slovak lowlands, reference numbers: 25, 65, 66.

Table 2.2 Spring and autumn densities of hares, shown with type and intensity of farming, field sizes, climatic and hunting (killing or removal) information; ordered by farm type. Mean (minimum-maximum) or mean ± standard deviation values for densities and field sizes are given when available, otherwise mid-range (minimum-maximum) is shown, or the value as provided by the authors without indication of range. Climatic data were obtained from the Times Atlas of the World (1980) and www.eventsworldwide.com, unless provided by the author (•) or by Ricci (1983; ♦). Symbols indicated data from counts: in summer (†), in winter as well (‡), on pasture only (§). A = August temperature; ■ = same site before and after farming intensity was reduced.

Farm type	Intensity of farming	Spring density (hares 100 ha^{-1})	Autumn density (hares 100 ha^{-1})	Method used to estimate density	Field size (ha)	Mean January temp (°C)	Mean July temp (°C)	Mean annual precipi-tation (mm)	Hunt-ing?	Source
Arable	High		42.8 ± 14.2	Clearance netting	118	-1•	18a•	500•	Yes	Andrzejewski & Jezierski (1966)
Arable	High		57 ‡	Belt assessment	big	-2	19	550	Yes	Jezierski (1968)
Arable	High	36		Belt assessment	143	-1•	18a•	500•	Yes	Pielowski (1969)
Arable	High	14				0	21	600	Yes	Bertoli (1975)
Arable	High	30	50			-1•	18a•	500•	Yes	Pielowski (1975)
Arable	High	30.5	45.3	Belt assessment	"tens"	-1•	18a•	511•	Yes	Bresinski (1976a)
Arable	High	30.7 (27.3-33.9)	51.7 (42.7-65.9)	Clearance counts		-1•	18a•	500•	Yes	Bresinski & Chlewski (1976)
Arable	High		43.0 (41.8 & 44.8)	Belt assessment		-1•	18a•	500•	Yes	Bresinski (1983)
Arable	High	28.8 (22.6 & 34.9)	64.5 (52.2-70.9)	Clearance counts	17.0 (3.5-40.8)	2	20	750	Yes	Pépin (1985; 1987)
Arable	High	27.7 (27.1 & 28.3)	44.2	Spotlight counts	0.8 (0.3-2.0)	0	16	840	Yes	Späth (1989)
Arable	High	23.1 (16.2-29.9)	32.3 (16.7-47.8)	Belt assessment		-2	19	550	Yes	Pielowski (1990)
Arable	High ■	38.4	60.4		51.1	2	20	592•	Yes	Slamečka (1991)
Arable	High	36.8	65.7		57.0	2	20	592•	Yes	Slamečka (1991)
Arable	High	58 (51-67) ‡	104 (96-113)	Spotlight counts	9 (3-15)	0	16	840	Yes	Spittler (1992)
Arable	High	Low	Low	Day transect counts	<200	<-4•	19	525•		Lewandowski & Nowakowski (1993)
Arable	High	15 (10-20)		Spotlight counts, clearance counts	10	4•	18•	750	Yes	Reitz & Leonard (1994)
Arable	High	9.6 (5.2-17.2)	12.3 (4.0-26.9)	Spotlight counts	90 (30-150)	0	16	950	Yes	Ahrens *et al.* (1995)
Arable	High		25 (20 & 30)	Spotlight counts	20	5	14	1000	Yes	Marboutin & Aebischer (1996)

Arable	High	21.0 (9.9-29.2)	11.5 (4.8-18.1)	Spotlight counts		0	16	840	Yes	Nösel & Ahrens (1996)
Arable	High	12.9 (9.3-18.2)	10.8 (3.1-24.7)	Spotlight counts		0	16	500	Yes	Ahrens & Kotwitz (1997)
Arable	High	32.7 (31.0 & 34.3)	47.2 (32.3-65.0)	Spotlight counts		0	20	625	Yes	Klansek *et al.* (1998)
Arable	High		8.3 (3-13)	Spotlight counts		2	20	750	Yes	Marboutin *et al.* (2003)
Arable	Intermediate		17 ‡	Belt assessment	medium	-2	19	550	Yes	Jezierski (1968)
Arable	Intermediate	116				0	21	600	Yes	Bertoli (1975)
Arable	Intermediate ■	66.5	97.9		37.6	2	20	592●	Yes	Slamečka (1991)
Arable	Intermediate	57.6 (46.3-64.7)	76.5 (59.3-102.3)	Spotlight counts		0	20	625	Yes	Klansek *et al.* (1998)
Arable	Low	32.3	45.2	Belt assessment	"a few"	-1●	18a●	511●	Yes	Bresinski (1976a)
Arable	Low	24.5 (20.8-27.2)	29.0 (24.6-31.4)	Belt assessment	1	-2	19	550	Yes	Wasilewski (1991)
Arable	Low	~ 2x above	~ 2x above	Day transect counts	<8.5	-4●	19	575●		Lewandowski & Nowakowski (1993)
Arable	Various		18 (8-28)	Belt assessment	11.6 (5.6-17.5)	-2	19	550	Yes	Panek & Kamieniarz (1999)
Arable		77 (67-91)	163 (137-196)	Spotlight counts		-2	18	550	Yes	Frylestam (1979)
Arable §		Stock fields 4, unstocked 52		Dawn and dusk counts		3	17	575		Barnes *et al.* (1983)
Arable		24.0 (16.5-35.7)		Spotlight counts		0	16	840	Yes	Pegel (1986)
Arable			13.9 ‡	Spotlight counts	19.5	3	17	575	Yes	Stoate & Tapper (1990)
Arable			51 (40-65)	Spotlight counts	1.7	2●	19●	680●	No	Bray (1998)
Arable			14 (12-15)	Spotlight counts	2.0	2●	19●	680●	Yes	Bray (1998)
Arable		5.6	5.9	Spotlight counts		0	16	950	Yes	Ahrens (2000)
Arable		82 (48-112)	121 (78-204)	Spotlight counts		0	20	537	Yes	Hackländer *et al.* (2001)
Arable & mixed			32 (0-63)	Spotlight counts		3	17	575		Tapper & Barnes (1986)
Mixed	High	107 (46-164)	183 (89-339)	Clearance netting	5.6	0●	17●	550●	No	Abilgard *et al.* (1972)
Mixed	High	26 (13-36) ‡		Spotlight counts	5.7	3	17	575	No	Bradshaw (1993)
Mixed	High	101 (98 & 104) ‡		Spotlight counts	7.8	3	17	575	No	Bradshaw (1993)
Mixed	High	3.2	4.85 ‡	Spotlight counts, twilight counts		3	17	575	No	Langbein *et al.* (1999)
Mixed	Intermediate	11.3 ± 3.7	19.8 ± 18.4	Clearance netting	1.2 (0.5-3.3)	1	24	1000	No	Meriggi & Alieri (1989)
Mixed	Intermediate		30.0 ± 16.6	Clearance netting	1.5 (0.4-5.9)	1	24	1000	No	Meriggi & Alieri (1989)

Mixed	Intermediate	5.1 (2.5 & 7.6)		Spotlight counts	15.6 (11.0-20.0)	2	20	892●		Verheyden (1991)
Mixed	Intermediate	4.4		Clearance counts	2	5♦	21♦	659♦	No	Pépin & Cargnelutti (1994)
Mixed	Intermediate	1.5		Clearance counts	2	5♦	21♦	659♦	Yes	Pépin & Cargnelutti (1994)
Mixed	Intermediate		21	Spotlight counts		2	20	750	Yes	Marboutin *et al.* (2003)
Mixed	Low	13	9 †	Day counts	5.5	3	17	575	Yes	Rothschild & Marsh (1956)
Mixed	Low		13 ‡	Belt assessment	small	-2	19	550	Yes	Jezierski (1968)
Mixed	Low		45.3 ± 32.0	Clearance netting	1.0 (0.3-2.2)	1	24	1000	No	Meriggi & Alieri (1989)
Mixed		28.4 (16.3-40.6)		Belt assessment	48 (<100)	-2	19	550	Yes	Pielowski (1966)
Mixed		45 (38-55) ‡	59 (54-62)	Spotlight counts		-2	18	550	Yes	Frylestam (1979)
Mixed			10	Spotlight counts	18	3	17	575		Tapper & Barnes (1986)
Mixed		19.5 (18.9 & 20.0)	37.6 (37.5 & 37.7)	Spotlight counts, belt assessment		1	24	1000	Yes	Prigioni & Pelizza (1992)
Mixed		13 (4-27)	33.5 (26.8-36.8) ‡	Belt assessment, day transects, twilight & spotlight counts		3	17	575	No	Langbein *et al.* (1999)
Mixed		11.0 (6.2-16.3)	44.6 (40.6-51.1) ‡	Belt assessment, day transects, clearance, twilight & spotlight counts		3	17	575	Yes	Langbein *et al.* (1999)
Pasture	Low	12.2 (8.7-16.3)		Dawn counts	73	-2	18	550	Yes	Frylestam (1976)
Pasture	Low	14 (14-15)	19 (16-24)	Spotlight counts		-2	18	550		Frylestam (1979)
Pasture	Low	4.6 (2.7 & 6.4)		Spotlight counts	4.1 (1.5-6.6)	2	20	892●		Verheyden (1991)
Pasture	Low	1.4 (0.5-2.8)	8.0 ‡	Spotlight counts, twilight counts		3	17	575	No	Langbein *et al.* (1999)
Pasture		17.8 (17.5 & 18.1)	22.0 (21.7 & 22.3)	Spotlight counts		0	16	725		Fehlberg (1997)
Pasture		2	4.5 (4.0 & 5.0)	Spotlight counts		0	20	625	Yes	Klansek *et al.* (1998)
Various	Various	60 (11-108)		Spotlight counts	3.2 (0.4-6.0)	0	16	840	Yes	Petrak (1990)
Various	Various		4.3 (2.5-7.1)	Day transect counts		3	17	900	Yes	Hutchings & Harris (1996)
Various	Various		41.7 (11.0-145.3)	Spotlight counts		0	16	754	Yes	Eskens (1999)
Various	Various	19 (3-83)	25.0 (1.2-147.4)	Spotlight counts		0	16	950	Yes	Kilias & Ackermann (2001)
Various	Various	10 (0-19)		Spotlight counts		0	17	975	Yes	Pfister (2002)

Farm type, intensity of farming and hunting had no significant effect on autumn density (arable 48 ± 37 hares 100 ha^{-1}, n = 30; mixed 29 ± 17 hares 100 ha^{-1}, n = 11; Table 2.3). Results show that although there is no significant difference between hare numbers in arable and mixed habitats in autumn, by spring hare numbers are lower in mixed habitats than in arable habitats. Data analysed suggest that field size, precipitation, temperature and hunting do not affect hare numbers.

Table 2.3 Results of ANCOVA on spring and autumn hare density in which farm type (arable or mixed), intensity of farming (intermediate or high) and hunting (yes or no) were between-group factors. *df* = degrees of freedom; MS = mean square; * = interaction term.

	Source of variation	***df***	**MS**	***F***	***P***
Log (spring density)	Farm type	1	1.811	17.946	< 0.001
	Intensity	1	0.034	0.338	0.567
	Farm type* Intensity	1	1.335	13.232	0.001
	Error (between group)	22	0.101		
Log (autumn density)	Farm Type	1	0.217	1.580	0.217
	Error (between group)	35	0.137		

2.3.2 Effects of habitat and climate variables on demographic parameters

The effects of habitat and climate variables on demographic parameters could not be analysed statistically because of small sample sizes (Table 2.4 and Table 2.5). Table 2.5 shows the mean for each of these parameters for different farm types (arable and mixed) and different intensities of agriculture (low, intermediate and high). Parameters could not be compared between hunted and non-hunted areas, as carcasses from shoots were used to derive the parameters in all but one study. As total sample sizes for numbers of litters, numbers of leverets per litter and adult survival were < 6, data were not included.

Table 2.4 Population parameters shown with farm type and intensity of farming; ordered by farm type. Mean (minimum-maximum) values are given when available, otherwise mid-range (minimum-maximum) is shown, or the value as provided by the authors without indication of range. Data are derived in winter, which is the hunting season (for the previous breeding season in the case of breeding parameters); those derived from a different season are indicated: autumn (†), whole year (‡), breeding season (§). "Young" are defined in various ways by different authors, but most frequently as hares < 1 year old. ● = a population not usually hunted; ♦ = data combined for analysis.

Farm type	Intensity of farming	Sex ratio (% females)	% females breeding	Mean no. litters/ female/ year	Mean no. leverets/ litter	No. leverets/ female/year	Age structure (% young)	% young surviving	% adults surviving	Source
Arable	High	51					38			Jezierski (1968)
Arable	High	52 (49-55)		3.2	2.3	7.4 (6.5-9.0)	50 (36-61)	23	95, 81§	Pielowski (1975; 1976)
Arable♦	High	58				4.3 (2.3-6.2)	68 (57-76)			Pépin (1978)
Arable♦	High	52				4.8 (3.4-6.0)	71 (70-72)			Pépin (1978)
Arable♦	High	52				4.9 (3.0-9.9)	69 (62-80)			Pépin (1978)
Arable	High	57 (57-58)				7.2 (6.8-8.0)	70	52 (46-63)	62 (40-73) §	Frylestam (1979)
Arable	High	50					55			Bresinski (1983)
Arable	High	51	94			9.4	61 (55-71)	37 (23-50)	82, 40 (35-45) ‡	Pépin (1987; 1989)
Arable	High	56					50 (47 & 52)			Späth (1989)
Arable	High		85			7.5	48 †	20 (16-23) §	94, 68§	Pielowski (1990)
Arable	High		90 †			12.5	42 †	30 †	49 ‡	Marboutin & Péroux (1995)
Arable	High	52					28			Nösel & Ahrens (1996)
Arable	High	50					29			Ahrens & Kotwitz (1997)
Arable	High		96 (92-100)	5.2	2.8 (2.7-2.9)	14.5 (13.9-15.0)	59 (49-69)	20 (14-25)		Marboutin *et al.* (2003)
Arable	Intermediate	48	68	3.4	2.3	7.8			53 ‡	Raczynski (1964); Andrzejewski & Jezierski (1966)
Arable	Intermediate	62					47			Jezierski (1968)

Farm type	Intensity of farming	Sex ratio (% females)	% females breeding	Mean no. litters/ female/ year	Mean no. leverets/ litter	No. leverets/ female/year	Age structure (% young)	% young surviving	% adults surviving	Source
Arable	Low	54 (50-57)	55 (52-57)			7.4	32 (21-39)	11 (6-14) §	85 (85-87), 77 (64-85)§	Wasilewski (1991)
Arable		49				3.5 (3.0-4.0)	66 (62-69)			Pépin (1978)
Arable							26 (16-36)			Ahrens *et al.* (1995)
Arable			83			8				Hackländer *et al.* (2001)
Mixed●	High	45 (33-57)				3.0 (1.4-5.0) †	50 (24-73)	50 (30-69)	59 (45-82) ‡	Abildgard *et al.* (1972)
Mixed	High	55 (50-58)				8.2 (7.7-8.8)	55	24 (19-26)	60 (38-79) §	Frylestam (1979)
Mixed	Intermediate		81 (79-86)	2.3 (1.9-2.5)	2.2 (1.0-2.1)	5.1 (4.1-5.9)	38 (32-41)	26 (19-31)		Hansen (1992)
Mixed	Intermediate		95 †	4.9	2.6	12.8	66 †	29 †		Marboutin *et al.* (2003)
Pasture	Low	48 (48-58)				8.6 (8.4-8.9)	53	19 (18-20)	66 (50-87) §	Frylestam (1979)

Table 2.5 Demographic parameters for different farm types and intensity of farming; figures are mean (minimum-maximum) and *n* = sample size.

		Sex ratio (% females)	% females breeding	No. leverets/ female/year	Age structure (% young)	% young surviving
Farm type	**Arable**	53 (48-62)	82 (55-96)	8.2 (3.5-14.5)	48 (26-70)	27 (11-52)
		n = 13	*n* = 7	*n* = 11	*n* = 16	*n* = 7
	Mixed	50 (45 & 55)	88 (81 & 95)	7.3 (3.0-12.8)	52 (38-66)	33 (24-50)
		n = 2	*n* = 2	*n* = 4	*n* = 4	*n* = 4
Intensity of farming	**Low**	54	55	7.4	32	11
		n = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1
	Intermediate	62	88 (81 & 95)	9.0 (5.1 & 12.8)	50 (38 & 66)	28 (26 & 30)
		n = 1	*n* = 2	*n* = 2	*n* = 3	*n* = 2
	High	51 (45-56)	87 (68-96)	8.4 (3.0-14.5)	46 (26-69)	29 (20-50)
		n = 10	*n* = 5	*n* = 8	*n* = 13	*n* = 6

Table 2.6 Habitat and other variables and their association with hare abundance: positive (+), negative (–), neutral (neu), or assumed positive (ass.+); ordered by country; maize *Zea mays*. Positive associations: in summer only ([1]), for all seasons except winter ([2]), when there are ≤ 10 habitats 100 ha^{-1} ([3]), when ≤ 40% of the area is pasture ([4]).

Country	Arable	Pasture	Wheat	Cereals	Rape	Beet	Legumes	Maize	Field size	Monoculture	Habitat density	Habitat heterogeneity	Fallow land	Woods	Wood edge / hedge	Temperature	Precipitation	Predators / foxes	Hunting	Method	Source
Austria	neu		neu				neu						neu	neu		neu	–			Spotlight counts	Hackänder *et al.* (2001)
Bulgaria									–	–		+		+				–	–	Hunting bag	Petrov (1976)
Bulgaria									neu									–	–	Hunting bag	Ninov (1990)
Denmark																+	–[1]	neu		Hunting bag	Andersen (1952)
Denmark																+	–			Hunting bag	Rattenborg (1991)
France		–	+	+											–					Clearance counts	Pépin (1985; 1987)
France	+		+			+	+													Radiotracking	Marboutin & Aebischer (1996)
France																		neu		Spotlight counts	Marboutin *et al.* (2003)
Germany																+	–	–	ass. +	Hunting bag	Spittler (1976)
Germany	+	+	+	+		+				–				–	+				ass. +	Hunting bag	Schropfer & Nyenhuis (1982)
Germany									neu		neu								ass. +	Hunting bag	Mayer (1983)
Germany		neu		neu		neu	neu	neu	neu			neu	neu		neu	+	–	neu	neu	Spotlight counts	Pegel (1986)
Germany																	–			Hunting bag	Spittler (1987)
Germany		+		–				–	–			+	neu		+					Spotlight counts	Späth (1989)
Germany	neu	+[4]		neu		neu	neu	neu	neu		+	+	+	neu	neu	+	–	neu	neu	Spotlight counts	Petrak (1990)
Germany																	–			Spotlight counts	Spittler (1992)

Country	Arable	Pasture	Wheat	Cereals	Rape	Beet	Legumes	Maize	Field size	Monoculture	Habitat density	Habitat heterogeneity	Fallow land	Woods	Wood edge / hedge	Temperature	Precipitation	Predators / foxes	Hunting	Method	Source
Germany				+														–		Spotlight counts	Ahrens *et al.* (1995)
Germany																+	–		ass. +	Hunting bag	Nyenhuis (1995)
Germany		+		–[1]	–	+	+	–				+									Schäfers (1996)
Germany									neu	–	+	+					–	–	ass. +	Hunting bag	Spittler (1996)
Germany													+	+	+				–	Hunting bag, day counts, spotlight counts	Schneider & Maar (1997)
Germany					–					–		+								Spotlight counts	Eskens (1999)
Germany		–		+		–		+											ass. +	Hunting bag	Nyenhuis (1999)
Germany	+		+	+								+	+	–		+[1]				Spotlight counts	Kilias & Ackerman (2001)
Hungary	+	–	+			+							+	–			–[1]		ass. +	Hunting bags	Szederjei (1959)
Hungary								–		–		+									Bertoti (1975)
Italy		+		neu		neu		–	–			neu	+	neu		+				Clearance netting	Meriggi & Alieri (1989)
Italy		+	+	+			+	neu					+	+						Spotlight counts, belt assessment	Prigioni & Pelizza (1992)
Poland												+	+		+					Belt assessment	Pielowski (1966)
Poland	+	–					–													Belt assessment	Jezierski (1973)
Poland									neu											Belt assessment	Bresinski (1976a)
Poland													+	neu	–					Clearance counts	Bresinski & Chlewski (1976)
Poland																+	–[1]			Belt assessment	Bresinski (1976b)
Poland									neu				+	+	+					Clearance netting	Bresinski (1983)
Poland									–	–				–		+			ass. +	Hunting bag	Pielowski (1990)

Country	Arable	Pasture	Cereals	Wheat	Maize	Legumes	Beet	Rape	Field size	Monoculture	Habitat density	Habitat heterogeneity	Fallow land	Wood edge / hedge	Woods	Temperature	Precipitation	Predators / foxes	Hunting	Method	Source
Poland								–	–	–		+	+							Day transect counts	Lewandowski & Nowakowski (1993)
Poland									–	–			+	–	–			–	ass. +	Hunting bag, belt assessment	Panek & Kamieniarz (1999)
Slovakia																+	–				Hell (1969)
Slovakia									–	–	+	+	+								Slamečka (1991)
Slovakia									–	–		+				+	–[1]	–	–		Slamečka *et al.* (1997)
Slovakia, Austria	+	–										+	+							Spotlight counts	Klansek *et al.* (1998)
Sweden		+	+		+		+			–		+						+	–	Spotlight counts	Frylestam (1979; 1980a)
Sweden		+	+	+	+	+							+							Spotlight counts	Frylestam (1992)
Switzerland																+[2]	–[1]		ass. +	Hunting bag	Eiberle *et al.* (1982)
Switzerland																+[2]	–[1]		ass. +	Hunting bag	Eiberle (1984)
Switzerland	+			+								+	+	–	+					Spotlight counts	Pfister (2002)
UK	+	–												–						Day counts	Rothschild & Marsh (1956)
UK											+	+								Radiotracking	Tapper & Barnes (1986)
UK	+	–		+	+	+					+[3]	neu	+	–	+				+	Day transect counts	Hutchings & Harris (1996)
UK	+	–	+	+	+	+	+	neu	+		–	+	+	+				–	+	Relative abundance as Percieved by farmers	Vaughan *et al.* (2003)

Once data were split by habitat type and farming intensity, small sample sizes made it difficult to interpret how these factors affect population parameters (Table 2.5). The data were also derived using different methods. However, demographic parameters did vary with habitat: the survival rate of young appears to be higher in mixed habitats than in arable habitats for example (Table 2.5). Data also suggest that birth rates are higher in areas of intermediate farming intensity than in those of low or high intensity.

The proportion of females breeding was positively correlated with precipitation (Spearman's rank correlation coefficient $r_s = 0.732$, $P = 0.025$, $n = 9$) and with mean January temperature (females breeding: $r_s = 0.732$, $P = 0.025$, $n = 9$). The proportion of young in the population was positively correlated with July temperature (Pearson correlation coefficient, $r = 0.603$, $P = 0.005$, $n = 20$). Results suggest that fecundity and survival are affected by habitat type and intensity of farming, and by climate.

2.3.3 Associations with habitat, climate, predator numbers and hunting

Variables identified by studies as being positively associated with density are arable habitats, including various crop types and fallow land, and temperature (Table 2.6). In contrast, monoculture, precipitation and predators are negatively associated with density (Table 2.6). Field size was identified as being negatively associated with hare numbers in half of the studies, and neutral in the others. The association between hare numbers and pasture and woodland depends on spatial scale.

2.4 Discussion

2.4.1 Associations with habitat

Hares are positively associated with arable habitats, but the nature of their association with pastural habitats is less clear. In general, when pasture makes up a small proportion of the landscape, its effect is positive, but wide-ranging pasture has a negative effect (Petrak 1990; Hutchings & Harris 1996). This is shown by the lower hare densities in pastural landscapes than in mixed and arable habitats, and may help to

explain why mixed habitats have lower densities than arable habitats. Even in mainly arable areas, pasture can be negatively associated with density (Pépin 1985, 1987; Marboutin & Aebischer 1996; Table 2.6). The variation in density with habitat type that I found throughout Europe agrees with findings of individual studies comparing densities in different habitat types (Frylestam 1979; Verheyden 1991; Hutchings & Harris 1996). However, my results showed that density was similar in arable and mixed habitats in autumn, but that in spring mixed habitats had lower densities than arable habitats, particularly in areas of intermediate intensity farming. This suggests that winter survival rate is lower in mixed habitats than in arable habitats. It also suggests that mixed habitats have higher birth rates and/or survival of young than arable areas, since they reach a similar density by the end of the breeding season.

Within arable and mixed habitats, winter wheat and other cereals are positively associated with hare abundance. Hares select cereal crops for foraging when the crops are in early stages of growth and suitable as food, but this preference declines as the crops develop (Tapper & Barnes 1986; see Chapter 3). Once no longer suitable as forage, cereals provide cover for hares (Tapper & Barnes 1986; see Chapter 3). Rape, beet and legumes Fabaceae all tend to be positively associated with hare density; maize appears to be neutral, or negatively associated with abundance where grown in large monocultures or with extensive use of pesticides (Bertoti 1975; Meriggi & Alieri 1989). Hares feed on all of these crops, although herbs and grasses make up the majority of their diet (Homolka 1987a; Chapuis 1990); non-cereal crops also provide cover for hares. In the interpretation of overall associations between hares and various factors, it is important to be aware that research in which no significant association was found is unlikely to be published. However, in all studies included in this review, associations with a range of factors were investigated meaning that neutral results are more likely to be reported alongside positive or negative associations (see Table 2.6).

Field size is either negatively associated with hare abundance or neutral (Table 2.6); analysis showed that there was no effect of field size on density. The only study in which hares were found to be positively associated with large fields only had 1% of fields > 20 ha in size (Vaughan *et al.* 2003), whilst those in the other studies ranged from 0.35 to 200 ha. At the extreme of increasing field size, extensive monoculture is negatively associated with hare abundance, although the studies include only one example of a real monoculture in which one crop covers the entire study site (Bertoti 1975). The study showed that following the conversion to a monoculture, hare density

was reduced by almost 90% (Bertoti 1975). In Bulgaria the decline of hares started at the same time, and in the same areas as monocultures of up to several square kilometres appeared (Petrov 1976). In such areas food availability decreases during the summer as crops reach maturity simultaneously (Frylestam 1980a, 1986; McLaren 1996), and alternative food resources are not available due to the loss of hedgerows and fallow land. In areas of monoculture hares are found near field edges where the vegetation is more diverse (Lewandowski & Nowakowski 1993).

A change in farm management to a monoculture results in a loss of habitat density and heterogeneity, which are both positively associated with hare abundance (Table 2.6). Hutchings & Harris (1996) found that increasing habitat density up to 10 habitats 100 ha^{-1} had a positive effect on hare numbers. The loss of heterogeneity caused by intensification may help to explain why arable areas that are intensively farmed have lower numbers of hares than those that are less intensively farmed. The only study in which the association of hare abundance and habitat density was found to be negative was that of Vaughan *et al.* (2003), but farms in this study consisted of up to 50 habitats 100 ha^{-1}. This suggests that optimal habitat densities exist for hares, and since data were representative of farms throughout England and Wales (Vaughan *et al.* 2003), that the scale of increases in field sizes and changes to monoculture in Britain have not caused the decline in its hare population. In areas of low landscape heterogeneity, hares are in poorer body condition, which may affect breeding success, and hares have lower survival rates than those in heterogeneous landscapes (Frylestam 1980a). Hansen (1998) found that although females in an enclosure farmed only for cereals had similar numbers of young to those in an area farmed for a diversity of crops, leverets had higher mortality rates in the cereal system.

Fallow land, including set-aside (land taken out of production for European Union subsidies) and areas with low level permanent cover, is associated with high hare abundance. Fallow land creates heterogeneity at the between- and within-field scale, and provides hares with food and cover throughout the year (Frylestam 1992; Vaughan *et al.* 2003). Woodland and hedgerows also provide cover for hares, although the influence of woodland habitats on hare numbers depends on the spatial scale. Small woodlands in a predominantly agricultural landscape are positive for hares (e.g. Schneider & Maar 1997; Vaughan *et al.* 2003), but if the area of wood is large it can be negatively associated with hare numbers. This may be due to the provision of cover for foxes (Bresinski & Chlewski 1976; Pielowski 1990; Panek & Kamieniarz 1999).

2.4.2 Associations with climate

The effect of climate variables on hare numbers is complex and depends on the time of year. This may explain why no effect of climate on density was found. However, in general, temperature is positively associated with abundance (e.g. Andersen 1952; Meriggi & Alieri 1989; Nyenhuis 1995; Table 2.6). Mild temperatures, particularly during the winter, reduce the energy needs of hares (Hackländer *et al.* 2002a), and lead to higher pregnancy rates, increased litter sizes, and a longer breeding season (Hewson & Taylor 1975). However, they also increase infection rates of diseases (Eiberle, Matter & Wettmann 1982; Eiberle 1984). Results showed an increase in the proportion of females breeding with increased winter temperature. Adverse weather conditions, such as very low temperatures, or moderate temperatures with high precipitation, cause mortality in leverets, particularly during the first two weeks of life (Hackländer *et al.* 2002a).

Precipitation is negatively associated with abundance, although very low rainfall during the summer may decrease hare numbers (Bresinski 1976b; Eiberle *et al.* 1982; Slamečka *et al.* 1997). Frylestam (1979) found that if rainfall was low during summer months, birth rate declined, and suggested this was due to low food availability. This may explain the positive relationship I found with the proportion of females breeding. However, wet weather not only increases the energy demands of thermoregulation, particularly in leverets, but also increases the prevalence of diseases such as coccidiosis (Edwards *et al.* 2000) and pseudotuberculosis (Barre, Louzis & Tuffery 1978).

2.4.3 Associations with predators and hunting

Abundance of predators, mainly foxes, is negatively associated with hare abundance (e.g. Spittler 1996; Panek & Kamieniarz 1999; Vaughan *et al.* 2003; Table 2.6). Erlinge *et al.* (1984) estimated that in southern Sweden predators consumed at least 40% of the annual production of hares. A simulation model based on data from southern England also suggested that predation can substantially limit hare population growth and density (Reynolds & Tapper 1995). Hunting bag data suggest that where fox numbers are reduced by disease, hare numbers increase (Spittler 1976; Ninov 1990; Lindström *et al.*

1994) and as fox numbers recover hare numbers decrease (Spittler 1976; Lindström *et al.* 1994; Ahrens *et al.* 1995; Slamečka *et al.* 1997; Ahrens 2000). Similarly, an experiment showed that hare numbers increased when predators were killed in an area (Tapper, Brockless & Potts 1991).

The majority of authors who use hunting bags to investigate habitat associations of hares assume that the relationship between hunting and abundance is positive. This is borne out by the two studies in which the relationship was tested (Hutchings & Harris 1996; Vaughan *et al.* 2003). However, in Bulgaria hunting was reduced and then stopped in 1979 and 1980 because of low numbers; higher hare numbers resulted (Petrov 1976; Ninov 1990). Over-hunting is also considered a problem in parts of Germany (Schneider & Maar 1997). Results of my analysis showed no relationship between hunting and numbers of hares. This may be due to the range of densities and variation in levels of hunting in different European countries.

2.4.4 Changes in habitat, climate and predator numbers since 1960

High numbers of hares are associated with mild winters, low precipitation, low predator numbers, arable land, and habitat heterogeneity including a diversity of crops, some fallow land and small rather than large areas of pasture and woodland. To understand why hares have been declining since the 1960s it is important to identify whether the climate has become less favourable for hares, predator numbers have increased, or favourable habitats have decreased over the same time scale.

Since 1961 there has been a general increase in temperature, particularly during winter, of up to 2 °Celsius (°C) throughout Europe (Schönwiese & Rapp 1997), a change that should benefit hares rather than cause a decline. Precipitation has increased in western and parts of eastern Europe, and decreased in parts of central Europe (Schönwiese & Rapp 1997). The combined increase in winter temperature and precipitation may have increased rates of disease transmission over the last few decades (Barre *et al.* 1978; Eiberle *et al.* 1982; Edwards *et al.* 2000). However, climate alone is unlikely to have played a large role in the decline of hare populations.

Long-term studies of fox abundance are relatively scarce, and so hunting bag data are often used to assess population numbers (Chautan, Pontier & Artois 1998;

Sadlier *et al.* in press). Although hunting bag data suffer from bias and do not strictly reflect the numbers of foxes in an area (Sadlier *et al.* in press), these data are often considered indicative of long-term population trends (Chautan *et al.* 1998). Data, mainly from hunting bags, suggest that in some European countries fox populations are stable (e.g. Chautan *et al.* 1998; Webbon, Baker & Harris, in press), whereas in others populations have increased (e.g. Slamečka *et al.* 1997; Chautan *et al.* 1998; Panek & Bresinski 2002). Although predator pressure is increased where predator numbers are higher, predator numbers alone are not the only issue to consider. Landscape structure has a significant impact on the effects of predators on their prey (Schneider 2001; Seymour, Harris, & White 2004), and a reduction in habitat heterogeneity may be associated with an increased risk of predation (see Chapter 3). A study in Poland showed that hare density can be almost doubled by increasing habitat heterogeneity and permanent cover without manipulating fox numbers (Slamečka 1991).

Farmland habitats have changed significantly throughout Europe since 1960. Despite this, the area of arable land, which is associated with high numbers of hares, has remained stable (Figure 2.2.1). The area of permanent pasture, associated with low numbers of hares, has remained stable in some parts of Europe, and has declined in others such as the UK and Germany (Figure 2.2.2). This means that the loss of arable land, or the conversion of farmland to less favourable pastural habitat, cannot be the cause of the decline in hare numbers. The amount of fallow land has remained stable or has increased (Eurostat, Luxembourg).

In contrast to agricultural land use, yields have changed dramatically. Yields of crops such as cereals, rape, sugar beet and fodder beet have increased by 50-100% since 1955 (e.g. winter wheat, Figure 2.2.3). Unlike cattle numbers, which have declined by 20% since 1975 (Eurostat), sheep numbers have increased in the same European countries, by as much as 50% in the UK (Figure 2.2.4). The fact that the area of pastural land has decreased in some of these countries, suggests that stocking density has increased substantially. Use of fertilizers such as nitrogen has increased five fold throughout the European Union since 1960 (Anonymous 2003), bringing with it an increase in mechanization. Such changes illustrate the intensification of farming since the early 1960s, which also results in decreased crop and habitat diversity. My results show that hare density is lower where farming is very intensive and habitat heterogeneity is low (e.g. Bertoti 1975; Petrov 1976). A reduction in habitat

Figure 2.2 Changes in i) area of arable land, ii) area of pastural land, iii) yield of winter wheat and iv) number of sheep in European countries from 1955 onwards (Eurostat, Luxembourg); † indicates the axis for data from France and the UK.

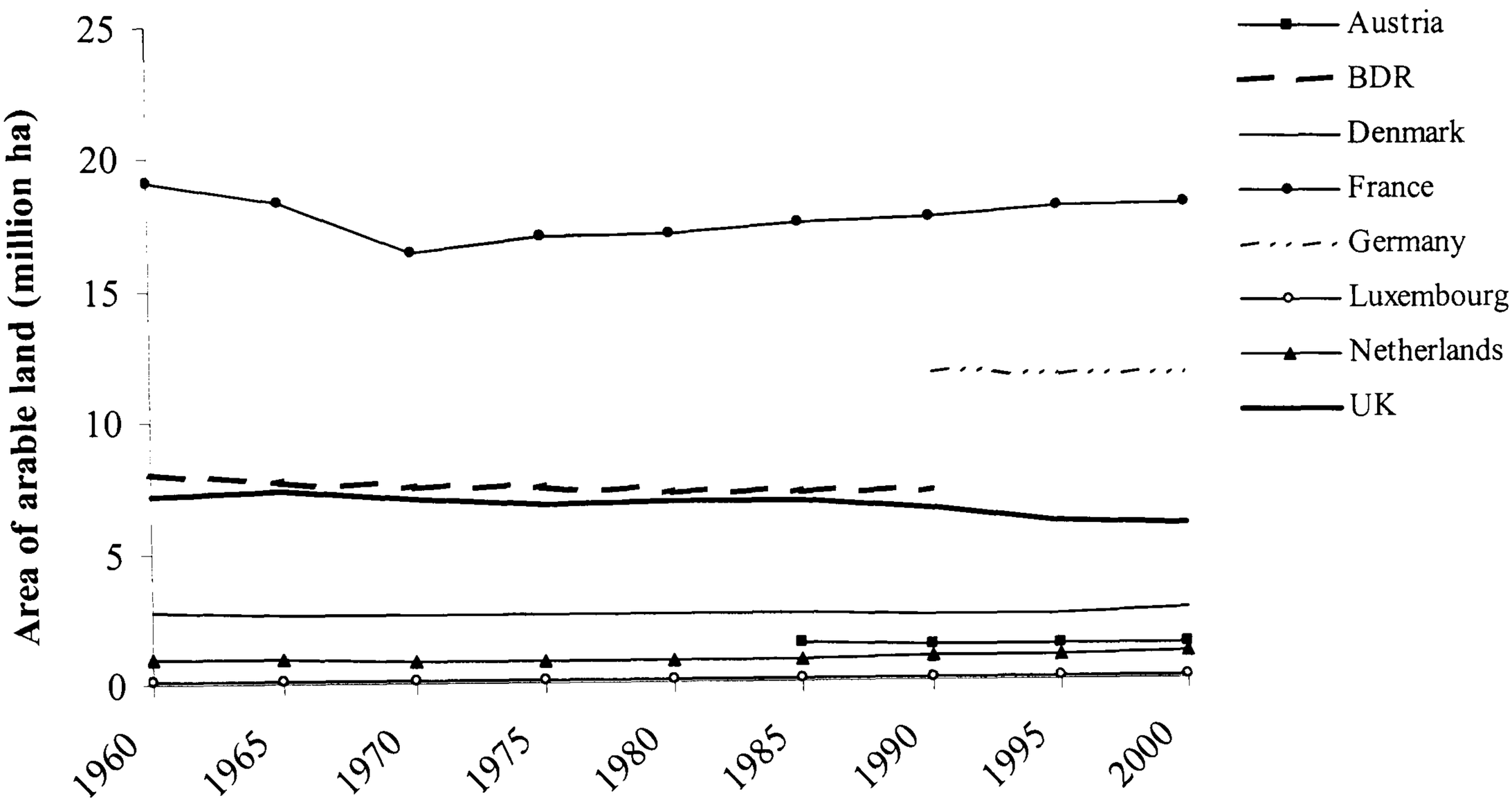

Figure 2.2.1

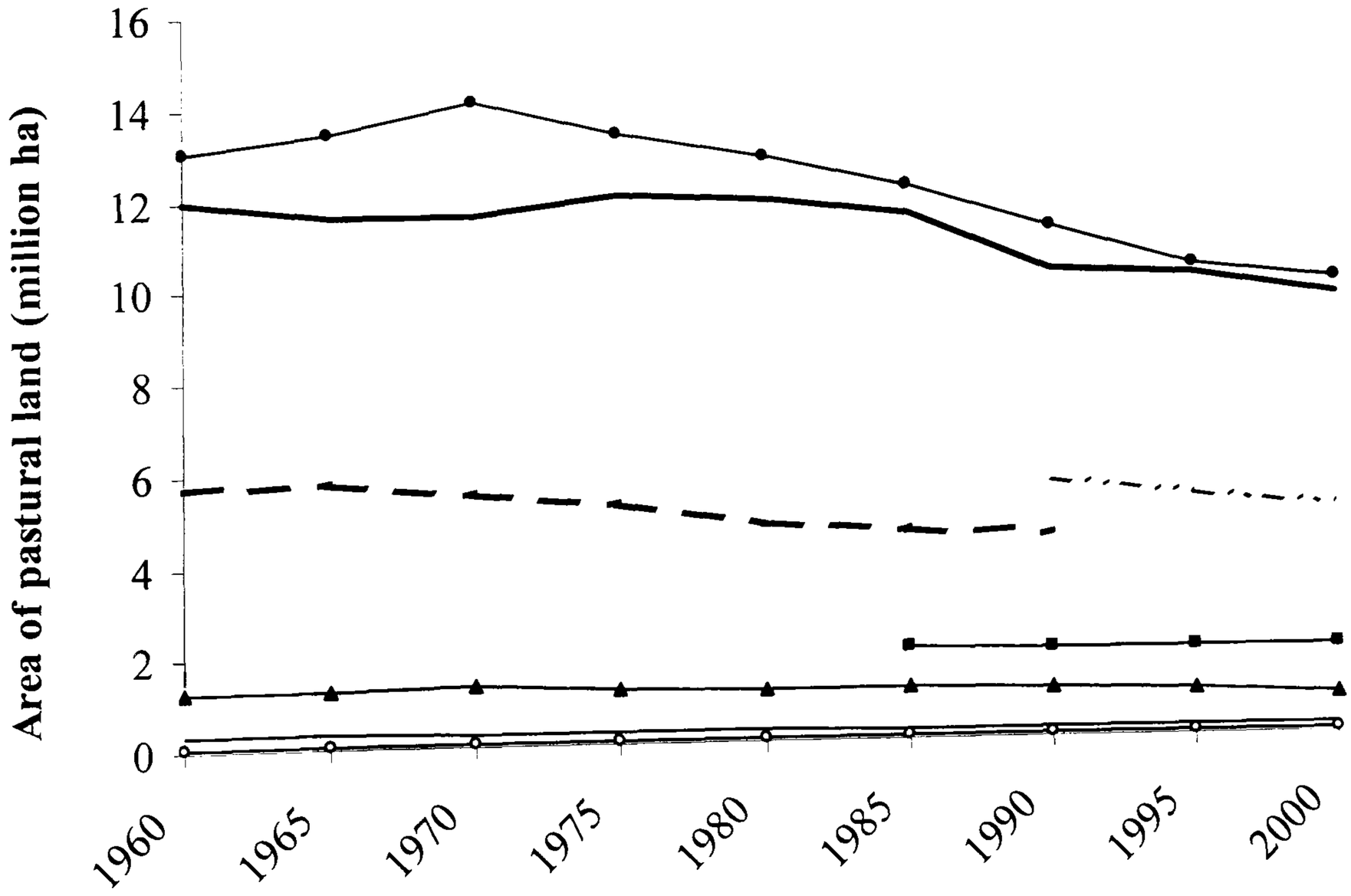

Figure 2.2.2

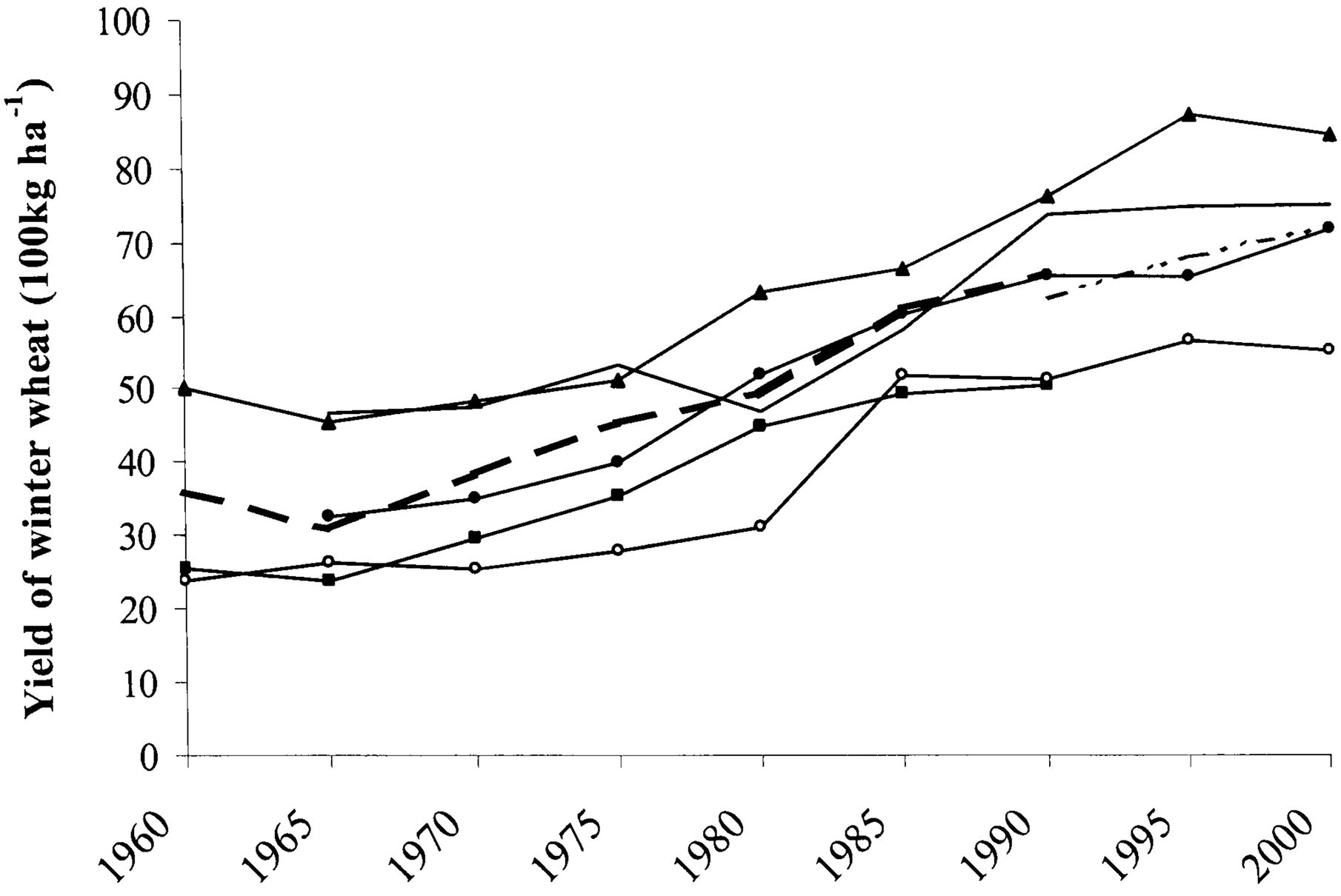

Figure 2.2.3

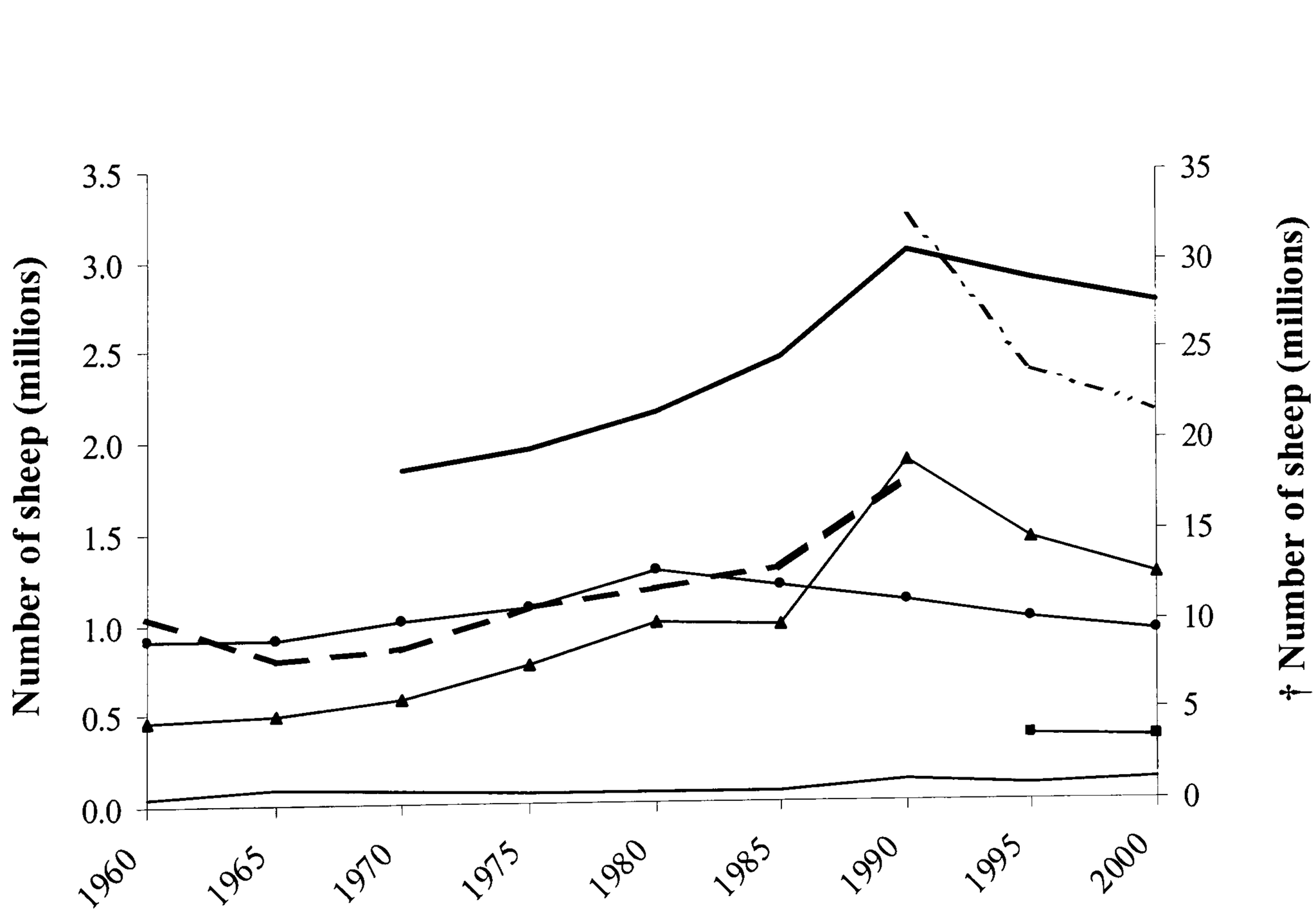

Figure 2.2.4

heterogeneity may lead to the loss of high quality year round forage and/or cover, so that hares are more susceptible to both predation and unfavourable weather conditions (see Chapter 3). The effects of any change in climate or predator numbers on hare numbers are therefore magnified by the changes in agricultural management.

2.4.5 Conclusions

Evidence suggests that habitat changes caused by agricultural intensification are the ultimate cause of the decline in hare numbers, largely due to a loss of habitat heterogeneity. Predators may also have played a role, but their effect on prey populations depends largely on habitat structure (Schneider 2001). Habitat management is therefore considered a better way to increase hare numbers than predator control (e.g. Slamečka 1991). To understand the effects of interactions between habitat structure and predators it is important to first identify how demographic parameters such as fecundity and survival are affected by changes in habitat. A better understanding of how changes in demographic processes affect population size is also required, as data are limited and conflicting. A field study showed that there was no difference in numbers of young produced by females in arable areas with high and low hare densities (Hackländer *et al.* 2001). A computer simulation model of a declining arable population suggested that population growth rate was more sensitive to adult survival than to recruitment, whereas the opposite was true for a population with higher recruitment levels (Marboutin & Peroux 1995). This suggests that declining arable populations are more sensitive to factors such as hunting than stable populations, since hunting increases adult mortality. However, over-hunting is considered to be an aggravating factor rather than the primary cause of population declines (Marboutin *et al.* 2003). In contrast to declining arable populations, recruitment was most important to the growth rate in a declining pastural population model (McLaren *et al.* 1997). This indicates that any changes in leveret survival rates, due to yearly fluctuations or due to changes in habitat or climate for example, could have detrimental effects on population numbers in pastural landscapes. In an arable landscape in France numbers of hares were found to go through short phases of significant increases and declines as leveret survival and female fecundity changed, without any changes in habitat or level of

predation (Marboutin *et al.* 2003). Phases of change of approximately eight years have been found in long-term hunting data from some British populations (Tapper 1992). This suggests that intrinsic factors, which are not yet understood, may also drive population dynamics; lagomorphs are particularly sensitive to local extinctions when populations become small (Soulé 1987).

In this chapter I highlight the need for additional data on population demographics from all habitat types to gain a better understanding of which parameters have the greatest effect on population declines (see Chapter 5). Research is required in pastural landscapes in particular as data on behavioural ecology and demography are scarce, meaning that it is not yet understood why hares are present at relatively low numbers in these habitats (see Chapters 3, 4 and 5).

Having established that published data from pastural landscapes are limited, in the next chapter I address the problem by investigating the habitat requirements of hares in a pastural landscape. My aim is to determine how hare populations are limited by habitat availability in pastural landscapes.

Chapter 3

Habitat selection by European hares in a pastural landscape: is habitat heterogeneity important?

Smith, R.K., Jennings, N.V., Robinson, A. & Harris, S. (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *Journal of Applied Ecology*, in press, is based on this chapter.

Habitat selection by European hares in a pastural landscape: is habitat heterogeneity important?

3.0 Summary

A seasonal radio-tracking study was used to investigate home range size and habitat selection in a predominantly pastural landscape. Selection was investigated by categorising habitats by type, and by structure in terms of vegetation height, and was quantified for active and resting hares. The aim was to determine the importance of heterogeneity at the between- and within-habitat scales. Winter and spring ranges were larger than summer and autumn ranges; mean home range size was 34 ha. Hares selected pasture grazed by cattle and fallow land in preference to arable crops throughout the year, except during the winter when crops were suitable as forage. Many of the habitats selected were heterogeneous in structure, and hares avoided short homogeneous vegetation such as pasture grazed by sheep. Hares selected habitats with taller vegetation during the spring and summer. Heterogeneity at the between-habitat scale was less important to hares than heterogeneity at the within-habitat scale in the pastural landscape studied. Hare populations in pastural landscapes may be limited by habitat availability in terms of cover.

3.1 Introduction

Knowledge about the habitat requirements of hares in pastural landscapes is limited, as studies have mostly taken place in arable areas where numbers are higher (see Chapter 2). Broad-scale studies have shown that high numbers of hares are often associated with arable crops and fallow land, in both arable and pastural landscapes (Hutchings & Harris 1996; Vaughan *et al.* 2003; see Chapter 2). On pastural farms hares are also associated with improved grassland and woodland (Vaughan *et al.* 2003). Broad-scale studies show which habitats are important to hares, but fine-scale studies are needed to gain an understanding of why particular habitats are important to the species. Such studies will provide a better understanding of why changes in habitat due to agricultural intensification have caused hare numbers to decline, and so will aid the development of conservation policy for the species.

A radio-tracking study in an arable landscape showed that hares selected cultivated areas and avoided non-cultivated areas (Marboutin & Aebischer 1996). On a mixed farm hares only selected crops when they had recently emerged, and often extended ranges to include habitat diversity (Tapper & Barnes 1986). Habitat heterogeneity at the landscape and farm scale is positively associated with hare numbers (see Chapter 2), and affects mortality and natality (Frylestam 1980b). However, heterogeneity at the within-field scale has not yet been investigated, despite the fact that it is greatly affected by the intensification of farm management (see section *1.3.1*).

In this chapter, I aim to identify the importance of specific habitats to hares in a predominantly pastural landscape. I use a radio-tracking study to investigate seasonal home range size and habitat selection by hares in relation to the heterogeneity of habitats at two spatial scales. In particular I test the hypotheses that heterogeneity is important i) at the between-habitat, or farm scale, by investigating whether hares select arable and fallow land within a pastural landscape, and ii) at the within-habitat, or field scale, by investigating the structure of fields selected by hares, in terms of vegetation height. The overall goal was to determine whether hare populations in pastural landscapes could be limited by habitat availability.

3.2 Methods

3.2.1 Study area

The study area consisted of mixed, but predominantly pastural, farmland (415ha) in the mainly pastural county of Somerset, south-west England (Ordnance Survey grid reference at centre of site: ST 275425). It lies within the Bridgwater Bay Site of Special Scientific Interest (SSSI), an area designated by the Government due to its diverse flora and fauna. The mean density of hares at the study site was: 13.0 ± 0.0 hares 100 ha^{-1} in March and 15.9 ± 1.5 hares 100 ha^{-1} in October based on point-sampling spotlight counts between autumn 2000 and spring 2003 (Péroux *et al.* 1998; Appendix 1). The density of hares at the site is high compared to that in other pastural areas (mean based on day counts during October to January: 3 hares 100 ha^{-1}; Hutchings & Harris 1996). The study population is subject to low levels of hunting with dogs in the form of coursing (hunting with sight hounds) and beagling (hunting with packs of scent hounds).

On average between August 2000 and September 2002, 23% of the study area was used for arable crops (wheat, barley, linseed, field beans, oilseed rape, and fodder beet; mostly winter grown and harvested in summer), 8% for grass ley (temporary grass cut up to three times annually for silage), and 6% for fallow land (including uncultivated margins around arable fields and set-aside). In all years, 63% of the area was semi-improved grassland (mostly used for livestock grazing, but some cut for hay in summer). The mean field size was 7.4 ± 2.7ha for arable fields, 6.2 ± 1.6 ha for grass leys, and 6.3 ± 2.7 ha for pastures (total n = 56 fields). These are relatively small: the average field size for pastural landscapes in Somerset and Dorset is 9.5 ha (Westmacott & Worthington 1997). Field enlargement may have been impeded as field boundaries are primarily ditches.

Detailed data on the habitat, including crop types, measurements of vegetation height (estimated average minimum and maximum) in each field, and dates of harvest for crops, hay, and silage were collected every two weeks during intensive tracking periods, and every month throughout the rest of the year. Livestock in each field were counted every week during intensive tracking periods, and once a month during the rest of the year. Cattle were the dominant livestock from spring to autumn; few were

present during the winter. The area of grassland classed as sheep pasture increased from 11% in spring and summer to 18% in autumn and 34% in winter. Livestock units (LSU) were calculated using the average LSU for each category of stock (age and reproductive state; Nix 2001) weighted according to the number in each category kept in England and Wales, as stock categories were not known during the study. Livestock densities at the site (median 0.9, range 0.0 - 8.2 LSU ha^{-1}) were typical for grassland in England and Wales (median 1.0, range 0.0 - 8.5 LSU ha^{-1}; Vaughan *et al.* 2003). Crops and other habitat features were plotted using digital maps (1:10000; Ordnance Survey scale raster maps), digital aerial photographs taken in July 1999 (Counties Revealed, Geoinformation group, Cambridge, UK), and Geographical Information System software (ArcView GIS, Environmental Systems Research Institute, Aylesbury, UK).

3.2.2 Capture techniques

Hares were captured between May 2000 and August 2002. Static nets and cage traps were used to minimise apparent sex and age biases which existed in each method of capture, and because the methods were suitable in different habitat types. When using static nets, 5 - 30 beaters flushed hares from cover into nets 2 - 30 m long set across gateways or other routes used by hares. This method could only be used in fields without livestock or mature crops. In total 32 females and 10 males were caught, on average 3.2 hares per day (n = 13 days).

Cage traps (single catch, single entry, spring door traps, 100 x 40 x 40 cm; Albi-traps, Wymondham, UK) were set in fields without livestock. Traps were unbaited, but the floor was covered with hay. They were checked at least once every 24 hours, soon after dawn, i.e. immediately following the period of activity of hares. In total 45 females and 42 males were caught using this method, averaging one hare per 16.6 trap-nights. A lower proportion of these hares were adults (60%) than those caught using static nets (83%). Adults were defined as hares > 7.7 months old and subadults 4 - 7.7 months; juveniles and leverets (< 4 months) are not considered here. Ages were determined by the presence or absence of an epiphyseal protrusion of the lateral ulnar knob (present in animals aged ≤ 234 days, i.e. 7.7 months; Stroh 1931), the hind foot length, skull length, and body weight (Bray, Champely & Soyez 2002; Hackländer *et al.* 2002a).

Hares captured were placed in cloth bags, sexed, aged and weighed. Each was fitted with two coloured and numbered plastic ear tags (Jumbotag or Rototag; Dalton, Henley-on-Thames, UK) and a radio collar (Biotrack, Wareham, UK). The combined weight of ear tags and collar was less than 5% of the body weight. Hares were released at the site of capture within 5 minutes of removal from the net or cage trap. During the study 15 - 30% of the population were radio-collared at any one time.

3.2.3 Data collection

Individual radio-collared hares were located at least 30 times during their active period (mainly at night) and 30 times during their inactive period (day), during each seasonal intensive tracking period. Active and inactive periods were defined following Holley (2001). Tracking seasons were defined as spring: intensive breeding (2 May – 12 June 2002); summer: some hares breeding (1 August – 5 September 2000 and 2002); autumn: no breeding (1 November – 13 December 2000); winter: early breeding (1 February – 13 March 2002; Lincoln 1974). Different hares were tracked in each season; spring: 6 females and 5 males; summer: 8 females and 3 males; autumn: 8 females and 3 males; winter: 5 females and 5 males. The majority of hares were collared during the month leading up to the intensive tracking periods (70%); others were collared between one and six months before intensive tracking commenced. Data were not collected during the first week after capture. Hares were located using a Suretrack STR 1000 receiver (Lotek Engineering, Ontario, Canada) and a three-element VHF Yagi antenna (Biotrack). Triangulation methods were used to locate each hare once during each inactive period, and usually once but up to a maximum of three times during each active period (each separated by at least 3 hours). Radio locations (fixes) were therefore discontinuous and independent (Harris *et al.* 1990), and were accurate to a 50 x 50 m grid. For each fix, information was collected about the vegetation type and height, and the number and type of livestock in the field. If a hare was not resting in its form when located during the day (< 1%) the fix was omitted from analysis. All fixes collected during the active period were included in analyses.

3.2.4 Statistical analysis

Home range size

For each hare, the 100% minimum convex polygon (MCP; Ranges V software, Centre for Ecology and Hydrology, Dorset, UK) was used to describe home range size, to allow comparison with earlier studies. These 100% MCPs will be referred to as 'home ranges'. Kernel methods, using least squares cross validation to select the smoothing parameter, were employed to estimate separate active and inactive 95% kernel range sizes (95% of fixes), which are referred to as 'ranges', and core areas (50% of radio fixes), which are referred to as 'core areas' throughout. These kernel estimates were used for all analyses, as this method provides robust estimates (Worton 1989; Seaman & Powell 1996; Animal Movement, United States Geological Survey - Biological Resources Division, Alaska Science Centre, USA; ArcView GIS 3.2). Range sizes were compared using repeated measures analysis of variance (ANOVAs), in which activity (active or inactive) was a within-subject factor, and season and sex were between-subject factors. Variables were transformed if necessary to conform to the assumptions of ANOVA (Zar 1999); sphericity (Mauchly's test) and homogeneity of variance (Levene's test) were checked for (Field 2000). All interaction terms were initially included, then where possible non-significant interaction terms were omitted and the analyses were repeated; results from the final models are shown here. Tukey post-hoc tests were used to compare means for seasons.

Habitat selection

Compositional analysis was used to compare utilised and available habitats at three levels during each season: a) range selection (active and inactive) within the study area, b) core area selection (active and inactive) within the study area, and c) habitat selection (active and inactive fixes) within ranges. Compositional analysis allows proportions describing the utilisation of each habitat category (which sum to one) to be analysed as independent data by log-ratio transformation. Tests for departure from random habitat utilisation were carried out using likelihood ratios. Habitats were then ranked in order of relative utilisation, and significant differences were identified (Aebischer, Robertson & Kenward 1993). Analysis was carried out using the 'Compositional Analysis Add-In Tool' (Version 4.1; Peter Smith, Wales, UK). Proportions of 'utilised' habitats equal to

zero were substituted by 0.001 (Aebischer *et al.* 1993). When comparing the availability and utilisation of habitats within ranges, if the availability for a habitat was zero for ≥ 50% of the individuals in a particular season it was excluded from analysis (Aebischer *et al.* 1993); approximately 2 were excluded per season. Not all individuals had all remaining habitats within their ranges, and hares with > 60% of habitats unavailable to them were also removed from analysis. Wilks' lambda (Λ) was calculated as a weighted mean for remaining proportions of 'available' habitats equal to zero (Aebischer *et al.* 1993). Data randomisation was used to calculate levels of significance because of the departure from multivariate normality of log-ratio difference distributions (Aebischer *et al.* 1993). Randomisation was based on 1000 iterations (Manly 1997).

For the investigation into habitat utilisation, habitats were classified in two ways. To investigate selection at the between-habitat scale, habitats were categorised by vegetation type (or use, in the case of pasture) using the following categories: pasture with sheep (0.06 - 1.15 Live Stock Units ha^{-1}), pasture with a low (0 - 0.99 LSU ha^{-1}), medium (1.00 - 1.99 LSU ha^{-1}) and high (> 2.00 LSU ha^{-1}) density of cattle, grass ley, cereal crops, non-cereal crops and fallow land. To investigate selection at the within-habitat scale, habitats were categorised by habitat structure in terms of vegetation height. Homogeneous vegetation was classified as: short (< 70 mm), medium (70 - 220 mm) and tall (> 220 mm). For heterogeneous vegetation, where the vegetation tended to be at two different heights, minimum and maximum heights were recorded: short/medium, short/tall, and medium/tall. In 67% of cases the maximum vegetation height covered the greatest area in the field, and the median percentage of vegetation at the maximum height was 75%.

Log-ratio data (transformed utilisation proportions) calculated during the compositional analysis were analysed using repeated measures ANOVAs in which activity was a within-subject factor, and season and sex were between-subject factors. Variables for which activity, season or sex had significant effects were then analysed using a doubly-multivariate repeated measures model (Field 2000). Pillai's trace test statistic was used, as it is robust to deviations from the assumption of equal population variances (Quinn & Keough 2002).

3.3 Results

3.3.1 Home range size

Home ranges calculated as 100% MCPs using both active and inactive fixes were similar in size to active ranges, as inactive ranges tended to fall within active ranges (Figure 3.1). Active ranges were significantly larger than inactive ranges (95% kernel ranges; active 36 ± 26 ha, inactive 19 ± 13 ha; Figure 3.1; Table 3.1). Ranges were significantly larger in winter and spring than in summer and autumn (Figures 3.1 and 3.2; Table 3.1).

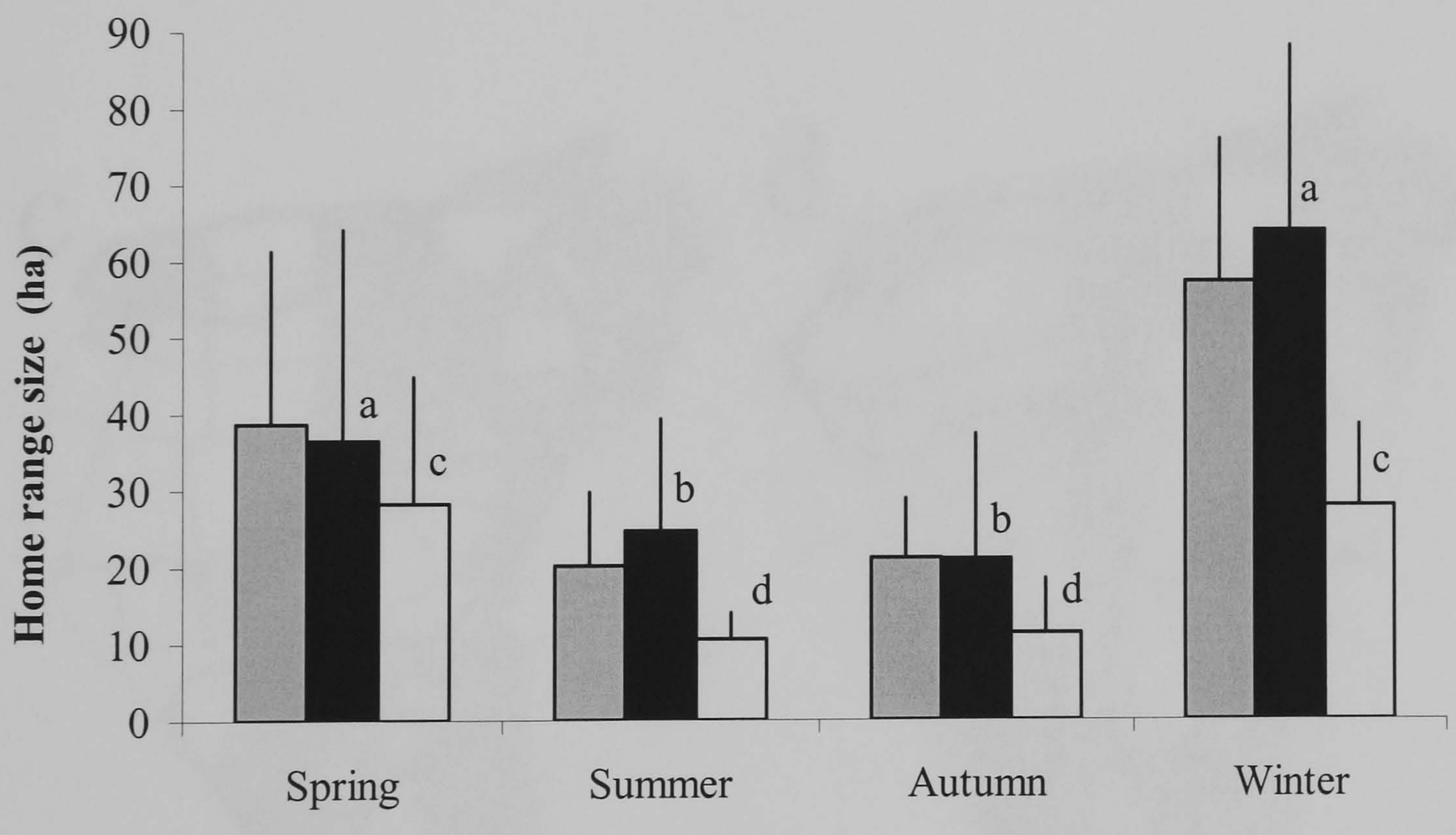

Figure 3.1 Mean home range sizes of adult and subadult hares in each season; sample size = 43. Grey bars are 100% MCP home ranges; black bars are 95% kernel active ranges; white bars are 95% kernel inactive ranges. Vertical bars show one standard deviation. Range sizes that are not significantly different from one another are indicated with the same lower-case letter.

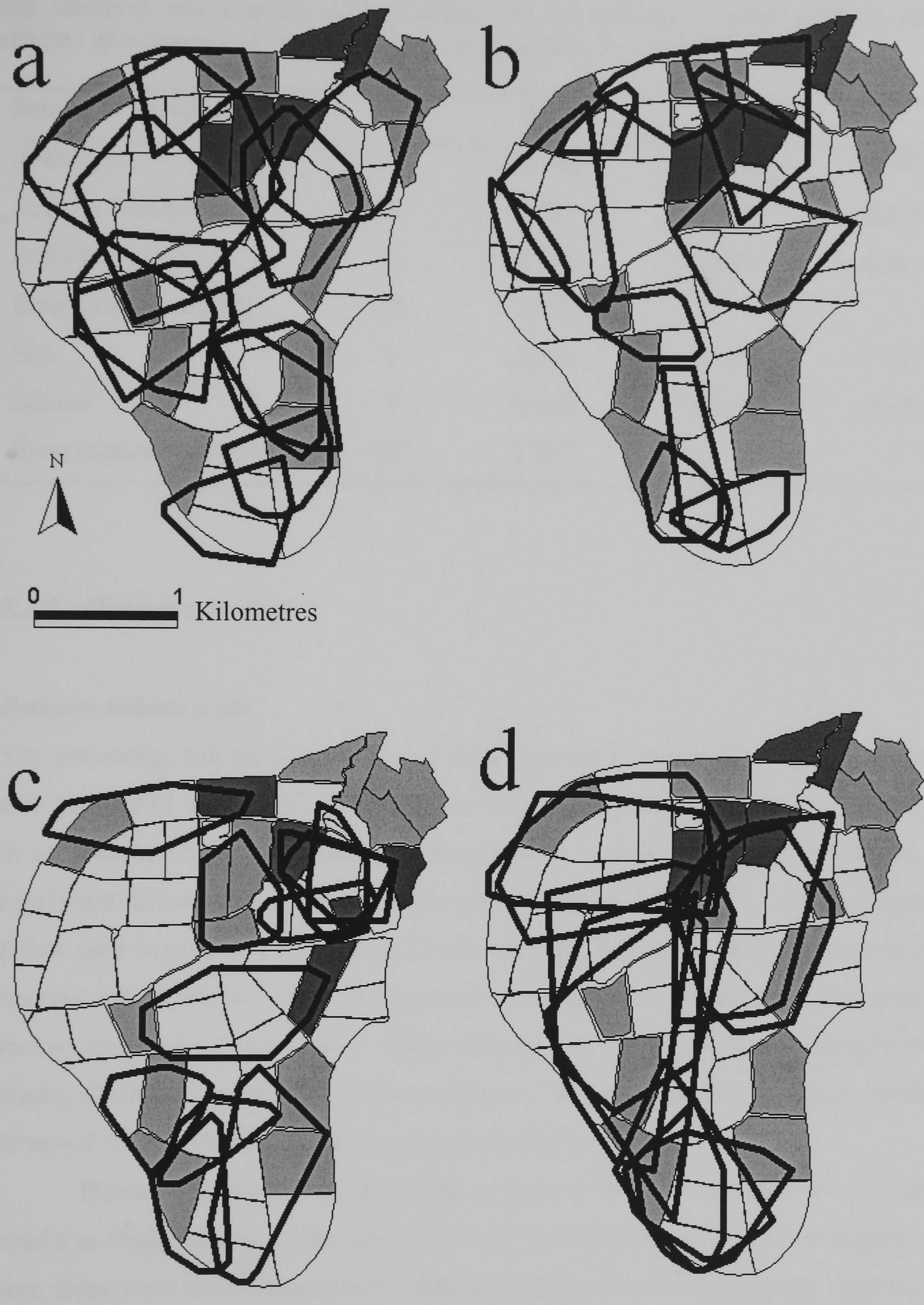

Figure 3.2 Home ranges (thick black lines = 100% MCPs, active and inactive fixes) of adult and subadult hares in each season (sample size = 43): a = spring, b = summer, c = autumn, d = winter. Arable crops are shown as light grey, grass leys as dark grey, and pastures (with and without livestock) as white. Field boundaries are shown as thin black lines.

Table 3.1 Repeated measures ANOVA on home range size in which activity (active and inactive) was a within-subject effect and sex and season were between-subject effects. *df* = degrees of freedom; MS = mean square; * = interaction term.

Source of variation	*df*	MS	*F*	*P*
Activity	1	50.732	33.149	< 0.001
Activity * season	3	3.735	2.440	0.079
Activity * sex	1	2.522	1.648	0.207
Error (within-subject)	38	1.530		
Sex	1	3.043	2.480	0.124
Season	3	15.402	12.552	< 0.001
Error (between-subject)	38	1.227		

3.3.2 Habitat selection

Between-habitat scale

The percentage habitat composition of ranges (utilised) compared to that of the study area (available) was significantly different from random for active and inactive ranges in all seasons (Table 3.2). Habitats were ranked in order of relative utilisation, and significant differences between habitats were identified (Table 3.3). Cattle pasture and fallow land were ranked higher than all other habitats for active and inactive hares in all seasons except winter, when sheep pasture ranked above fallow land, and grass ley ranked highest for active hares. Sheep pasture was one of the least selected habitats during all other seasons. There was no selection for pasture with a particular density of livestock (low, including no cattle, medium or high).

Habitat composition of core areas compared to the study area showed similar results to those for range selection. The main differences were that the composition of core areas were not different from random for active hares in spring and summer, and that ley was ranked higher than pasture and/or fallow land in autumn rather than winter (Table 3.3). Since results for ranges and core areas were similar, further analyses and discussion of habitat selection focuses on ranges, as the wider habitat use is considered important for management implications.

Table 3.2 Compositional analysis: results of MANOVA. The habitat composition of 95% kernel ranges (active and inactive), in terms of vegetation type, was different from random within the study area in all seasons.

		df	Wilks' Λ	χ^2	*P*
Active	**Spring**	6	0.029	38.954	0.004
	Summer	7	0.072	29.019	0.046
	Autumn	5	0.074	28.635	0.007
	Winter	5	0.039	32.415	0.010
Inactive	**Spring**	6	0.029	39.149	0.006
	Summer	7	0.066	29.850	0.033
	Autumn	5	0.098	25.552	0.012
	Winter	5	0.110	22.111	0.019

To investigate whether there was an effect of activity, season, or sex on habitat selection for ranges, the three log-ratio variables for which one or more factors showed significant effects (sex showed none; significance level 10%) were entered into a doubly-multivariate repeated measures model. Low, medium and high cattle density categories were combined, so that seasons were comparable. The model showed a significant overall effect of activity (Pillai's trace = 0.221, $F = 3.412$, $df = 3$, $P = 0.028$) and season (Pillai's trace = 0.514, $F = 2.618$, $df = 9$, $P = 0.009$), but no effect of sex (Pillai's trace = 0.067, $F = 0.862$, $df = 3$, $P = 0.470$), the activity * season interaction (Pillai's trace = 0.096, $F = 0.417$, $df = 9$, $P = 0.924$) or the activity * sex interaction term (Pillai's trace = 0.060, $F = 0.764$, $df = 3$, $P = 0.522$). Therefore, selection of habitats for ranges depended on whether the hares were active or inactive, and on the season.

The comparison of fixes (utilised) with habitat composition of ranges (available) showed that habitat utilisation was significantly different from random only for active hares in autumn and winter, and for inactive hares in spring (Table 3.4). Where selection was significantly different from random, habitats were ranked in order of relative utilisation, and significant differences between habitats were identified (Table 3.3). Selection of habitats in autumn (active) and spring (inactive) were similar to the selection of ranges described above. However, cereal, which was selected least

Table 3.3 Habitat types ranked according to relative utilisation, most utilised is at the top of the list: a) 95% kernel ranges versus total study area, b) 50% core areas versus total study site, c) fixes versus 95% kernel ranges. Habitat categories that are not significantly different from one another are indicated with the same lower-case letter. Non-cereal = non-cereal arable fields; NS = not significantly different from random utilisation.

a) 95% kernel ranges versus total study area

Active				Inactive			
Spring	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
High stock[a]	Low stock[a]	Low-Medium stock[a]	Ley[a]	High stock[a]	Low stock[a]	Low-Medium stock[a]	Low stock[a]
Fallow[ab]	Fallow[a]	Fallow[a]	Low stock[ab]	Low-Medium stock[ab]	Medium stock[a]	Fallow[a]	Sheep[ab]
Low-Medium stock[abc]	Medium stock[ab]	Ley[ab]	Sheep[ab]	Fallow[ab]	High stock[a]	Ley[ab]	Fallow[b]
Non-cereal[bcd]	High stock [abc]	Cereal[bc]	Fallow[ab]	Non-cereal[bc]	Fallow[ab]	Cereal[b]	Non-cereal[ab]
Cereal[cd]	Cereal[abc]	Non-cereal[c]	Non-cereal[ab]	Cereal[bc]	Ley[ab]	Non-cereal[b]	Cereal[b]
Ley[cd]	Ley[bc]	Sheep[c]	Cereal[b]	Ley[c]	Cereal[ab]	Sheep[b]	Ley[b]
Sheep[d]	Sheep[bc]			Sheep[c]	Sheep[ab]		
	Non-cereal[c]				Non-cereal[b]		

b) 50% core areas versus total study area

Active				Inactive			
Spring	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
		Ley[a]	Low stock[a]	High stock[a]	Medium stock[ab]	Low-Medium stock[a]	Low stock[a]
		Low-Medium stock[ab]	Fallow[ab]	Low-Medium stock[ab]	High stock[a]	Ley[ab]	Sheep[abc]
NS	NS	Fallow[a]	Cereal[ab]	Non-cereal[ab]	Fallow[a]	Fallow[ab]	Non-cereal[abc]
		Non-cereal[b]	Ley[ab]	Cereal[ab]	Low stock[ab]	Non-cereal[b]	Fallow[b]
		Cereal[bc]	Sheep[ab]	Fallow[a]	Sheep[a]	Sheep[b]	Cereal[abc]
		Sheep[c]	Non-cereal[b]	Sheep[a]	Cereal[ab]	Cereal[b]	Ley[c]
				Ley[b]	Ley[a]		
					Non-cereal[b]		

c) Fixes versus 95% kernel ranges

Active				Inactive			
Spring	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
		Low-Medium stock[a]	Ley[a]	High stock[a]			
		Ley[a]	Cereal[a]	Low-Medium stock[ab]			
NS	NS	Fallow[a]	Low stock[b]	Fallow[b]	NS	NS	NS
		Cereal[a]	Sheep[b]				
			Fallow[b]				
			Non-cereal[b]				

by active hares in winter for ranges, was ranked second highest when selecting habitats within these ranges.

Table 3.4 Compositional analysis: results of MANOVA. Seasonal habitat utilisation (active and inactive fixes), in terms of vegetation type, was at random within 95% kernel ranges in all but three cases.

		df	**Weighted mean Λ**	***P***
Active	**Spring**	2	0.809	0.570
	Summer	4	0.367	0.732
	Autumn	3	0.160	0.031
	Winter	5	0.028	0.033
Inactive	**Spring**	2	0.399	0.041
	Summer	4	0.032	0.266
	Autumn	3	0.103	0.054
	Winter	3	0.501	0.835

Within-habitat scale

Habitat composition of ranges, in terms of habitat structure, compared to that of the study area was significantly different from random for active and inactive ranges in all seasons (Table 3.5). Habitat structures were ranked in order of relative utilisation, and significant differences between habitat structures were identified (Table 3.6). In spring and summer, medium/tall habitat ranked in the top two for active and inactive hares, but had one of the lowest ranks in autumn and winter. In autumn, medium and short/medium habitats ranked in the top two for active and inactive hares, and for inactive hares in winter. In winter, tall habitat ranked higher than short/medium habitat.

Habitat composition of core areas compared to the study area showed almost identical results to those for range selection, except that habitat composition of core areas was not different to random for hares in spring (Table 3.6). Further analyses focus on habitat selection for ranges rather than core areas.

Table 3.5 Compositional analysis: results of MANOVA. The composition of 95% kernel ranges (active and inactive), in terms of habitat structure, was different from random within the study area in all seasons.

		df	Wilks' Λ	χ^2	*P*
Active	**Spring**	5	0.062	30.617	0.007
	Summer	5	0.071	29.049	0.006
	Autumn	5	0.068	29.556	0.011
	Winter	5	0.031	34.703	0.011
Inactive	**Spring**	5	0.122	23.119	0.015
	Summer	5	0.004	61.027	0.002
	Autumn	5	0.193	18.091	0.043
	Winter	5	0.003	56.949	0.002

Four log-ratio variables for which activity or season had significant effects (sex showed none; significance level of 10%) on habitat selection for ranges were entered into a doubly-multivariate repeated measures model. The model showed a significant overall effect of activity (Pillai's trace = 0.283, $F = 3.460$, $df = 4$, $P = 0.017$) and season (Pillai's trace = 1.481, $F = 9.016$, $df = 12$, $P < 0.000$), but no effect of sex (Pillai's trace = 0.018, $F = 0.160$, $df = 4$, $P = 0.957$), the activity * season interaction (Pillai's trace = 0.376, $F = 1.324$, $df = 12$, $P = 0.215$) or the activity * sex interaction (Pillai's trace = 0.050, $F = 0.460$, $df = 4$, $P = 0.764$). Therefore, selection of habitats, in terms of structure, for ranges depended on whether the hares were active or inactive, and on the season.

The comparison of fixes with habitat composition of ranges showed that habitat utilisation was significantly different from random only for active hares in autumn, and for inactive hares in spring (Table 3.7). Where selection was significantly different from random, habitats were ranked in order of relative utilisation, and significant differences between habitats were identified (Table 3.6). Selection of habitats in autumn (active) was similar to the selection of ranges described above. However, the ranks of habitat structures within ranges in spring (inactive) were almost the opposite of those for the range within the study site for the same season.

Table 3.6 Habitats categorised by vegetation height (minimum/maximum; Med = medium) ranked according to relative utilisation, most utilised is at the top of the list: a) 95% kernel ranges versus total study area, b) fixes versus 95% kernel ranges. Habitat categories that are not significantly different from one another are indicated with the same lower-case letter. NS = not significantly different from random utilisation. Results for core areas versus total study area are not shown as they are the same as for 95% kernel ranges except that habitat utilisation was not different from random in spring.

a) 95% kernel ranges versus total study area

Active				Inactive			
Spring	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
Med/Tall[a]	Med/Tall[a]	Med[a]	Med[a]	Med/Tall[a]	Short/Tall[a]	Short/Med[a]	Med[a]
Tall[ab]	Short/Tall[ab]	Short/Med[a]	Tall[a]	Short/Med[ab]	Med/Tall[ab]	Med[a]	Short/Med[ab]
Short/Med[ab]	Tall[bc]	Short[ab]	Short/Med[ab]	Tall[ab]	Tall[bc]	Tall[ab]	Tall[ac]
Med[ab]	Med[bc]	Tall[b]	Short[bc]	Med[abc]	Short/Med[bcd]	Short[b]	Short/Tall[cd]
Short/Tall[b]	Short/Med[cd]	Med/Tall[b]	Short/Tall[c]	Short/Tall[bc]	Med[cd]	Med/Tall[b]	Short[bd]
Short[b]	Short[d]	Short/Tall[b]	Med/Tall[c]	Short[c]	Short[d]	Short/Tall[b]	Med/Tall[d]

b) Fixes versus 95% kernel ranges

Active			Inactive				
Spring	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
		Med[a]		Med[a]			
NS	NS	Short/Med[ab]	NS	Tall[ab]	NS	NS	NS
		Short[b]		Med/Tall[b]			
				Short/Med[b]			

Table 3.7 Compositional analysis: results of MANOVA. Seasonal habitat utilisation (active and inactive fixes), in terms of habitat structure, was at random within 95% kernel ranges in all but two cases.

		df	Weighted mean Λ	*P*
Active	**Spring**	3	0.343	0.189
	Summer	3	0.314	0.142
	Autumn	2	0.279	0.039
	Winter	2	0.443	0.104
Inactive	**Spring**	3	0.194	0.019
	Summer	2	0.456	0.098
	Autumn	2	0.949	0.807
	Winter	3	0.468	0.370

3.4 Discussion

3.4.1 Heterogeneity at the between-habitat scale

My data on seasonal changes in habitat selection suggest that hares selected a variety of habitats for both feeding and resting throughout the year, as found by Tapper & Barnes (1986). When habitats were suitable for both, hares often used the same one for feeding and resting, as found by Reitz & Léonard (1994) and Marboutin & Aebischer (1996). For most of the year hares did not select arable habitats in preference to other habitat types; instead they selected pasture grazed by cattle (0.0 - 8.2 LSU ha^{-1}) and fallow land, when foraging and resting. Of the 43 home ranges, 14% of ranges and 40% of core areas consisted entirely of pasture and fallow land, even though arable crops were available nearby, and covered 31% of the site. Ranges without arable crops did not occur during the winter, but 30% of winter core areas contained none. Hares only selected arable habitats (cereal and grass ley crops) in preference to others when crops were short and suitable as forage, a preference also found by Tapper & Barnes (1986).

In arable landscapes hares are associated with set-aside (Frylestam 1992; Hutchings & Harris 1996; Vaughan *et al.* 2003), although the presence of set-aside has

no effect on hare numbers in pastural landscapes (Hutchings & Harris 1996). In this study hares selected cattle pasture and fallow land (including set-aside) equally.

Although broad-scale studies have shown that high numbers of hares are associated with arable crops within pastural landscapes (Hutchings & Harris 1996; Vaughan *et al.* 2003), at the finer scale hares do not appear to be dependent on these habitats. This suggests that heterogeneity at the between-habitat scale is of limited importance to hares in the pastural landscape studied. However, where grassland is managed more intensively than at my study site, the vegetation is often short and homogeneous throughout the year (Stoate 1996; Vickery *et al.* 1999). In this case, the heterogeneity of habitat types available to hares may become more important in providing them with the resources they require, so that they rely on arable crops to a greater extent in these areas. In intensively farmed arable landscapes, where fields are very large, hares have much larger home ranges than in less intensive arable areas (Reitz & Léonard 1994; Marboutin & Aebischer 1996), suggesting that individuals increase their home ranges to include a variety of habitats.

A need for heterogeneity at the between-habitat scale in intensively managed pastural landscapes may be due to requirements for food. The mean home range size calculated fits the trend shown by other studies in agricultural landscapes, for home ranges to decrease in size as the landscape changes from intensively managed arable land to pasture (Table 3.8). This suggests either that home range size is limited by energy expenditure (Swihart 1986) or that hares in pastural landscapes have access to sufficient, diverse food supplies within a relatively small home range (see Chapter 4). I found that ranges were largest during winter, as did Reitz & Léonard (1994), and during spring. During the winter, vegetation growth is likely to be limited, and hares selected arable crops in addition to pasture and fallow land for forage. Hares may have needed to cover a larger area to gain access to arable crops (see Chapter 4). However, in spring, hares selected pasture and fallow land, not arable crops, and so were not limited by availability. In the summer and autumn, arable crops are not suitable as forage, and in autumn, as vegetation growth slows, forage availability is likely to be at its lowest, and yet ranges were small. Therefore, changes in forage availability do not appear to explain variations in range size; changes in forage quality are examined in Chapter 4. Behavioural changes may provide an explanation. At the beginning of the breeding season (winter), and during peak breeding (spring), females are searching for suitable

Table 3.8 Home range sizes of hares in agricultural landscapes determined by radio-tracking. Month = number of months animals were tracked; *n* = number of animals tracked; A = active home range; A + I = active and inactive fixes i.e.total home range.

Location	Habitat	% grass	Method of calculation	Months	*n*	Mean home range size (ha)	Source
France	Intensive arable land	< 11%	95% MCP	< 5	20	138 (A)	Marboutin & Aebischer 1996
France	Intensive arable land	< 6%	100% MCP	> 6	21	61 (A)	Reitz & Léonard 1994
The Netherlands	Arable land	-	100% MCP	1-4	3	39 (A)	Broekhuizen & Maaskamp 1982
Hungary	Agricultural land	-	100% MCP	1-6	12	37 (A+I)	Kovács & Búza 1988
Oxfordshire	Agricultural land	25%	100% MCP	2	85	25 (A)	Bradshaw 1993
England	Agricultural land	≈ 50%	90% isopleth	1-7	15	38 (A+I)	Tapper & Barnes 1986
England	Agricultural land	63%	100% MCP	1	43	29 (A)	This study
The Netherlands	Cattle pasture	majority	100% MCP	1-14	10	26 (A)	Broekhuizen & Maaskamp 1982

sites in which to give birth, and males are searching for females. Low levels of mating activity occur in summer and autumn (Lincoln 1974), when range sizes at my study site were small.

3.4.2 Heterogeneity at the within-habitat scale

A need for heterogeneity at all habitat scales may be due to requirements for cover rather than forage. In this study hares selected specific habitat structures over others, and this depended on whether they were foraging or resting, and on the time of year. During spring and summer, hares tended to select habitat structures with taller minimum and maximum vegetation heights than those selected during the autumn and winter. Many of the habitats selected were heterogeneous in structure with different minimum and maximum vegetation heights, although tall homogeneous habitats ranked fairly highly in all seasons. In all seasons except winter, but particularly during the spring and summer, hares avoided pasture grazed by sheep (characterised by a short homogeneous structure; Fuller & Gough 1999; Vickery *et al.* 1999; Benton *et al.* 2003) and all other habitats consisting of short, even vegetation. This suggests that during the main part of the breeding season, hares select habitat structures that provide cover from predators and unfavourable weather conditions, which is particularly important for the survival of leverets (Tapper & Parsons 1984). In Poland foxes consume more hares during the spring, when leverets are abundant, than during other months (Goszczynski & Wasilewski 1992). Leverets are vulnerable to low temperatures, and moderate temperatures combined with high precipitation (Hackländer *et al.* 2002a). Pastural landscapes tend to be in the west of Britain, and so are on average warmer and wetter (January temperature 4 - 10 °C, mean annual precipitation 600 - 2000 mm; Anonymous 1980) than arable landscapes (January temperature -1 - 4 °C, mean annual precipitation 400 - 1000 mm; Anonymous 1980). Weather conditions also influence the selection of resting habitats by adults; in sunny weather hares are twice as likely to use long crops than when it is raining (Tapper & Barnes 1986).

Results suggest that heterogeneity at the within-habitat scale is important to hares in a pastural landscape. The heterogeneous vegetation structure produced by different levels of cattle grazing pressure (up to densities of 8.2 LSU ha^{-1}) and by fields

used for hay, provided the habitat structures preferred by hares throughout the year. The exception was tall homogeneous habitat, which was also selected but which was provided by arable crops. Hares selected pastures regardless of cattle density, and did not appear to avoid cattle as suggested by previous studies (Frylestam 1976; Barnes *et al.* 1983). In intensively managed pastural land, where habitats tend to be more homogeneous throughout the year, hare populations are likely to be limited by habitat quality in terms of the availability of cover. In Poland, autumn densities of hares increased with the number of permanent cover areas (Panek & Kameniarz 1999). At my study site the hare population may have been limited by the availability of cover to some extent, as tall homogeneous habitats, which were selected in all seasons but summer, were not readily available to hares during the autumn and winter (mean 8% area of site).

3.4.3 Conclusions

Hares maintained relatively small home ranges, and made use of the variety of different vegetation types and vegetation heights available. The fact that hares had access to heterogeneous habitat structures, providing cover throughout the year, may help to explain why hare numbers at this site are relatively high for pastural landscapes. Results suggest that habitat heterogeneity at the between-habitat scale is of some benefit to hares, and may be more important in intensively managed pastural landscapes. This may explain why hare numbers are relatively high in pastural areas where some arable crops are present (Hutchings & Harris 1996). However, data collected during this study did not support the view that hare populations are limited by the distribution and abundance of arable habitats in pastural landscapes (Hutchings & Harris 1996; McLaren *et al.* 1997).

Results showed that hares in the pastural landscape studied select for heterogeneity at the within-habitat, or field scale. In arable landscapes numbers of hares are higher where there is set-aside (Hutchings & Harris 1996), which increases heterogeneity at the between- and within-habitat scale. Unimproved grassland, which has a heterogeneous structure, is strongly associated with high hare numbers in both arable and pastural landscapes (Hutchings & Harris 1996). Hares not only required

varying habitat structures when foraging and resting, but also selected habitat structures depending on season, suggesting that both spatial and temporal heterogeneity are important to the species at the within-habitat scale. Further research is required to investigate habitat utilisation, in terms of vegetation structure, and hare abundance in pastural landscapes with different levels of habitat heterogeneity.

Hares in pastural landscapes are in poorer condition due to higher energy expenditure than those in arable landscapes (Appendix 2). Therefore, they are likely to be more susceptible to mortality by predation, disease, exposure, and hunting by humans. Further studies are needed in order to identify the most common causes of mortality in hares in pastural areas, and the effects of vegetation structure on these.

My findings in this chapter indicate that population numbers of hares in pastural landscapes may be limited by habitat quality in terms of cover. In the next chapter I investigate whether populations are limited by habitat quality in terms of forage.

Chapter 4

Does forage quality explain habitat selection by European hares in a pastural landscape?

A manuscript based on this chapter has been submitted to *Acta Theriologica*:

Smith, R.K., Jennings, N.V., Tataruch, F., Hackländer, K. & Harris, S. Vegetation quality and habitat selection by European hares *Lepus europaeus* in a pastural landscape

Does forage quality explain habitat selection by European hares in a pastural landscape?

4.0 Summary

Chemical analysis of the nutritional quality of forage from five habitat types was carried out to determine whether hares select habitats that provide high quality forage, and whether nutritional quality explains seasonal differences in the active ranges of hares in a pastural landscape. The aim was to determine whether hare populations are limited by forage quality in a predominantly pastural landscape. Hares did not tend to select habitats of high nutritional quality, in terms of fat or energy, over those of low nutritional quality. Hares did not increase active range size as the overall energy content of the study site decreased; seasonal differences in active range size were not explained by nutritional quality. Pastural habitat is fairly stable in terms of nutritional quality through the year, and results suggest that hare populations in pastural landscapes are not limited by forage quality.

4.1 Introduction

Hares are thought to require a varied diet to fulfil their nutrient requirements, as they eat a wide variety of species (Homolka 1982, 1987a; Frylestam 1986; Tapper & Barnes 1986; Chapuis 1990). Although hares use crops as forage (Frylestam 1986; Homolka 1987a, 1987b; Chapuis 1990; McLaren 1996), particularly when the crops have just emerged (Tapper & Barnes 1986; see Chapter 3), they prefer wild plants to cultivated species in arable, mixed and pastural landscapes (Frylestam 1986). Landscape heterogeneity plays an important role in the population dynamics of hares (Frylestam 1980b; see Chapters 2 and 3). Habitat heterogeneity may not only provide good quality cover for hares (see Chapter 3), but may also ensure the availability of high quality forage throughout the year.

Plant diversity has declined in agricultural landscapes as management has become more intensive (Bunce *et al.* 1994; McCollin, Moore & Sparks 2000; see section *1.3.1*), meaning that hares may have to eat poor quality diets. In arable landscapes the diet of hares is of lower quality during April – June than during winter, being less digestible, and containing less protein (McLaren 1996). This suggests that food intake has to be increased to meet the costs of breeding, which is at its peak during spring (McLaren 1996). Other studies have suggested that hare populations are forage-limited during the summer, particularly in areas of monocultures, where all crops reach maturity at the same time (Frylestam 1980a, 1986). In comparison, studies by Homolka (1987b) and Chapuis (1990) suggest that dietary diversity is highest during the summer.

Hares prefer the parts of plants rich in fat (Brüll 1976; Homolka 1987a). Eating plants rich in fat not only increases energy assimilation, but may also enable animals to reduce foraging activity and the weight of food required, and therefore predation risk (Hackländer, Tataruch & Ruf 2002b). Dietary fat is particularly important to lactating females as they produce milk with a high fat content (Broekhuizen & Maaskamp 1980). This is because the post-natal development of precocial young such as leverets is energetically costly (Hackländer *et al.* 2002a). In hares, milk fat is produced mainly from dietary fatty acids rather than from *de novo* synthesis (Demarne *et al.* 1978). Females fed a low fat diet ate more than those on a high-fat diet, but still assimilated lower amounts of energy, had reduced milk energy content and produced less milk

when they had large litters (Hackländer *et al.* 2002b). A shortage of fat in the maternal diet can therefore lead to lower levels of recruitment. This, along with the potential for higher mortality rates of hares in poor body condition, means that low quality diets are likely to have important effects on population numbers.

Hares in pastural landscapes may be limited by the availability of good quality habitats for foraging, as they have less kidney fat and are smaller than hares in arable landscapes (Appendix 2). These differences in body condition are not due to differences in dietary quality because it is similar in hares in the two landscapes (Appendix 2). However, hares in pastural landscapes may need to expend more energy to obtain a similar quality diet to those in arable landscape. For example, they may need to range further, or select home ranges containing habitats of high quality forage. Mammals in habitats of lower productivity tend to have larger home ranges than those in habitats of higher productivity (Harestad & Bunnell 1979). Home range size and the selection of habitats by hares was investigated in Chapter 3. Here I carry out chemical analysis of the nutritional quality of forage in the same habitats in order to investigate i) whether hares select habitats containing forage of high nutritional quality over those containing forage of low nutritional quality in each season, and ii) whether seasonal differences in active range size can be explained by differences in nutritional quality. The overall aim is to determine whether the hare population at the pastural study site is limited by habitat in terms of forage quality.

4.2 Methods

4.2.1 Active range size and habitat selection

Data on seasonal active range size and habitat selection were obtained by radio-tracking 43 hares at the study site described in section *3.2.1*. Hares were located at least 30 times during their active period in the seasonal intensive tracking periods (for further details see section *3.2.3*). For descriptions of the methods used to determine 95% active kernel range sizes, and habitat selection using compositional analysis, see section *3.2.4*.

4.2.2 Vegetation sampling

Vegetation samples were collected from the study site during the last two weeks of each season, following each intensive radio-tracking period (see section *3.2.3*). Individual samples were taken from four different locations within each randomly selected field; each was collected from a random 1 m² within separate randomly chosen 50 m² grid squares in each field. Vegetation was cut 1 cm above the ground from a circle 10 cm in diameter at each location. Samples were weighed before freezing until further analysis. An average of 28 fields were sampled in each season, of which a mean of 73% were pasture fields. Non-pasture fields were categorised as grass ley, cereal crops, non-cereal crops and fallow land. Roots were not sampled as they make up a small proportion (2%) of the diet of hares (Homolka 1987b).

4.2.3 Habitat quality

The four individual samples from each field were pooled within each season. These field samples were weighed, oven dried at 55 °C for 48 hours (Hoffman *et al.* 1999), weighed again to obtain the dry weight, and milled to 1mm fragments using a Micro hammer mill (Culatti, Zürich, Switzerland). The number of field samples obtained from each habitat type during a particular season ranged from 1 - 15 depending on availability; dry samples < 6g from the same habitat were combined for analysis. A total of 95 field samples were analysed for: % crude protein, % crude fat and % carbohydrate content at the Research Institute of Wildlife Ecology, Vienna. Energy content was calculated using Atwater factors; the digestible energy of fat, protein, and carbohydrates were assumed to be 37.7, 16.7 and 16.7 kJ g^{-1}, respectively (for methods see Hackländer *et al.* 2002b).

4.2.4 Statistical analysis

The variation in nutritional quality in terms of both energy (kJ/g) and fat (%) due to habitat type was investigated by using analysis of variance (ANOVA); both habitat type

and season were between-group factors. Variables were transformed if necessary to conform to the assumptions of ANOVA (Zar 1999). All interaction terms were initially included in the model, and non-significant interaction terms were omitted in turn and analyses repeated; only results of the final analysis are given here. The composition of the energy within forage, in terms of proportions of protein, fat and carbohydrate, was also investigated with habitat and season.

To investigate whether hares selected the habitat containing the highest quality forage in each season, the mean energy and fat content of forage within each habitat type was ranked and compared to the rank order of habitat selection (see Table 3.3). Pastures with different cattle densities (low, medium, high) were combined here to produce one rank for cattle pasture, which was the predominant type of pasture at the site. Where a different habitat type e.g. fallow land was ranked between pasture of two cattle densities, fallow land and pasture were given equal ranks.

To determine whether seasonal differences in range size were related to seasonal changes in habitat quality, the overall nutritional quality (in terms of energy) of forage within the study site was calculated for each season. This was done by using the mean energy content per unit area of forage within each habitat and the total area of each habitat type available at the site during each season. The overall energy contents of forage within the study site in each season were then ranked for comparison with mean active 95% kernel range sizes for each season.

4.3 Results

4.3.1 Quality of habitats selected

Both habitat type and season had a significant effect on energy and fat content, as did the habitat*season interaction (Figures 4.1 and 4.2; Table 4.1). In summer hares selected the habitats (pasture and fallow land) containing forage with the highest energy content, although there was little difference between the energy content of forage within habitats (Figure 4.1; Table 4.2); non-cereal was not available at this time of year. In contrast, they selected the habitat (pasture) containing forage with the lowest energy content in spring, and showed no preference for non-cereal crops, which had the highest

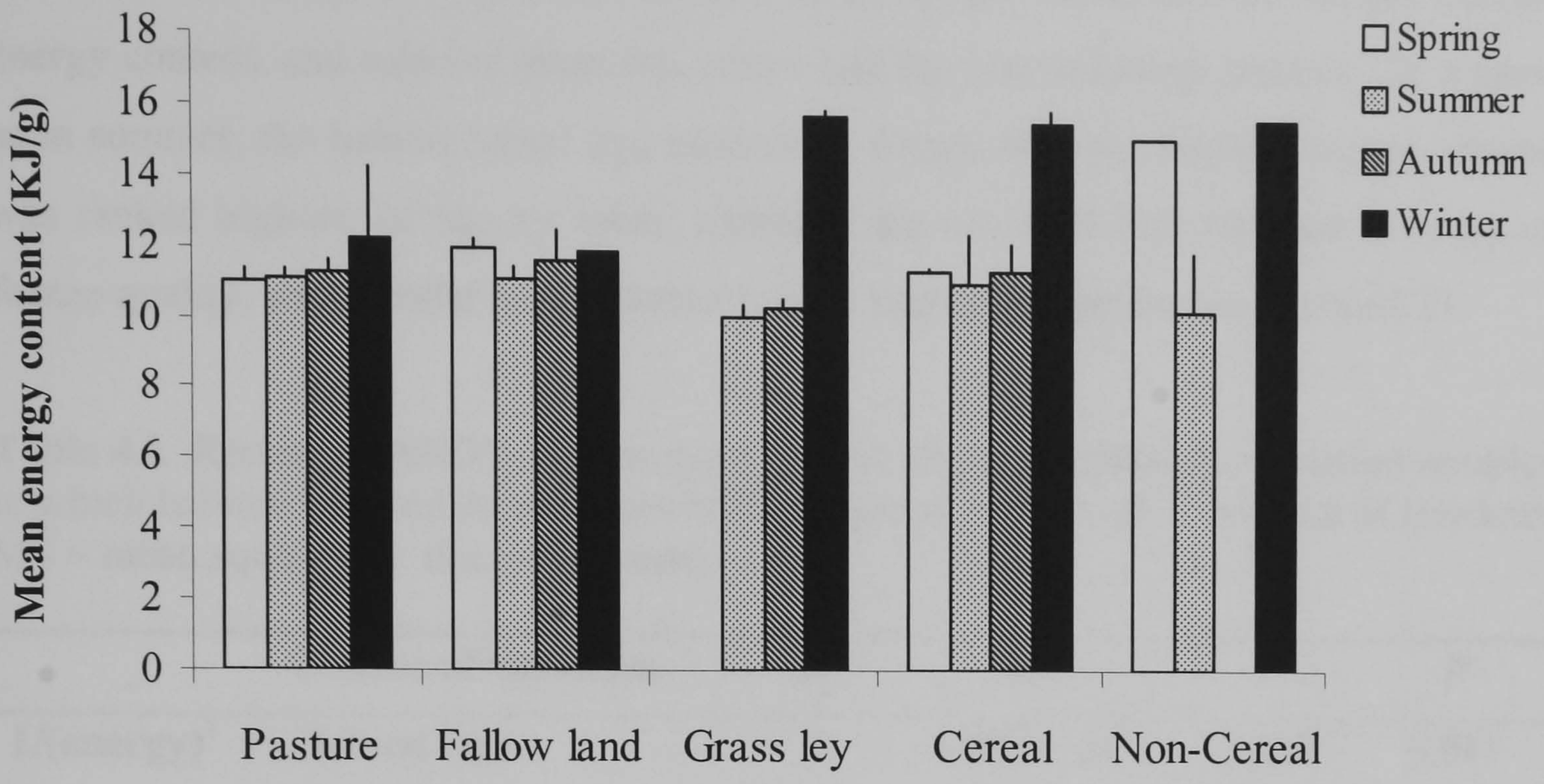

Figure 4.1 Mean energy content (kJ/g) of pasture, fallow land, grass ley, cereal and non-cereal habitats in relation to season. Vertical bars show one standard deviation. Missing data indicates a non-sampled habitat.

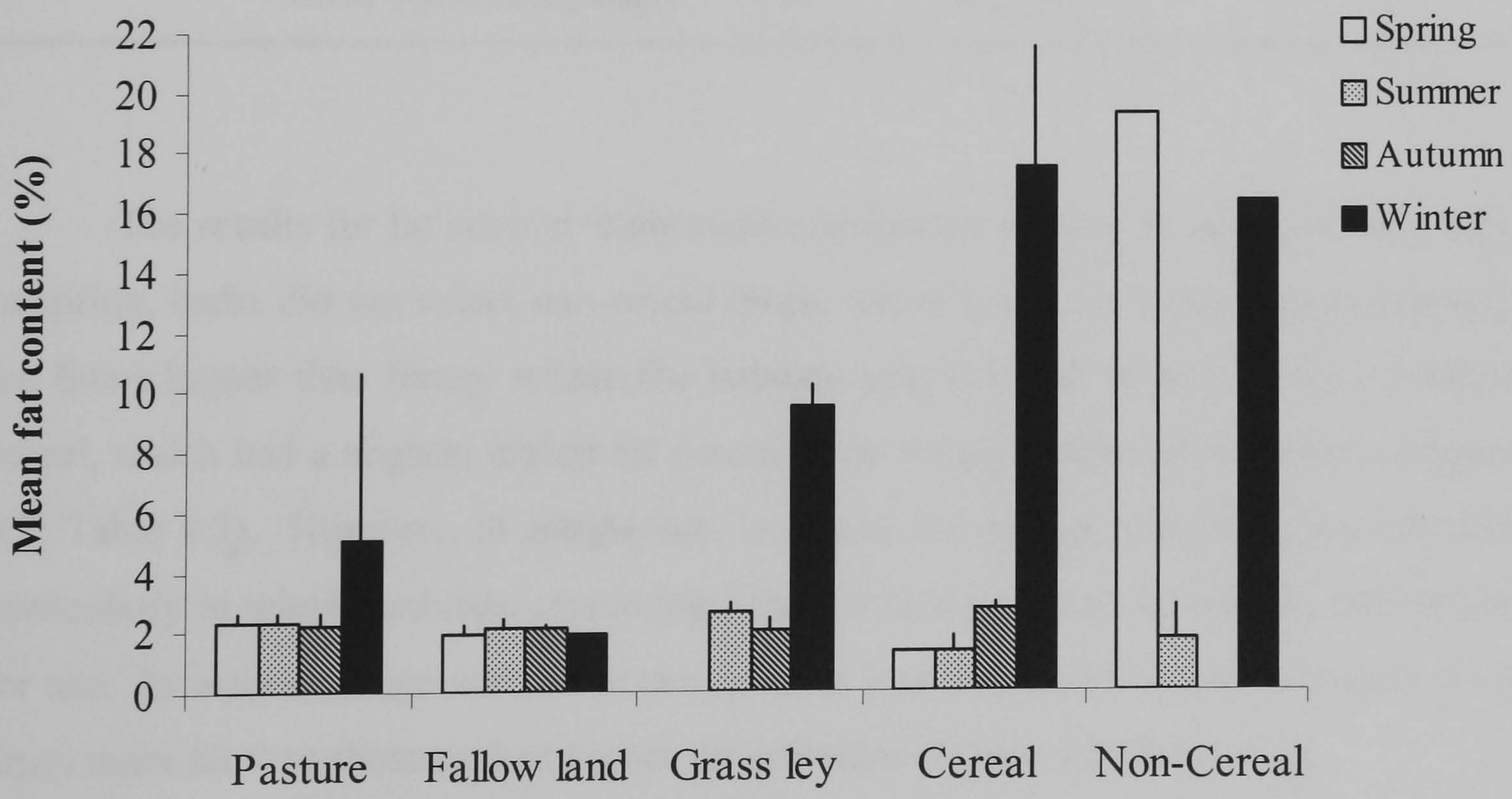

Figure 4.2 Mean fat content (%) of pasture, fallow land, grass ley, cereal and non-cereal habitats in relation to season. Missing data indicates a non-sampled habitat.

energy content (Table 4.2). In autumn, although energy content was fairly similar across habitats (Figure 4.1), hares avoided cereal crops, which had the second highest energy content, and selected grass ley, which had the lowest energy content. In winter, as in summer, the habitat (grass ley) containing forage with the highest energy content was ranked highest for use by hares, although the two next best habitats in terms of forage quality, with similar energy content, were ranked lowest for use (Table 4.2).

Table 4.1 Results of ANOVA on energy (kJ) and fat (%) content of vegetation samples in which habitat type and season were between-group factors. *df* = degrees of freedom; MS = mean square; * = interaction term.

	Source of variation	***df***	**MS**	***F***	***P***
1/(energy)^2	Habitat type	4	0.003×10^3	3.224	0.017
	Season	3	0.003×10^3	28.313	< 0.001
	Habitat type* season	10	0.006×10^3	6.143	< 0.001
	Error (between group)	77	0.010×10^3		
1/$\sqrt{}$fat	Habitat type	4	0.058	7.663	< 0.001
	Season	3	0.200	26.257	< 0.001
	Habitat type* season	10	0.092	12.000	< 0.001
	Error (between group)	77	0.008		

The results for fat content show some similarities to those of energy (Table 4.2). In spring, hares did not select non-cereal crops, which had a fat content approximately ten times higher than forage within the habitats selected, and in autumn they avoided cereal, which had a slightly higher fat content than forage within other habitats (Figure 4.2; Table 4.2). However, in comparison to results for energy content, in summer and particularly in winter, habitats containing forage with the highest fat content ranked low for use. In winter, forage within the two habitats least selected had approximately 2 - 9 times more fat than those ranked higher for selection (Figure 4.2; Table 4.2).

Most of the energy from forage in pasture, fallow land and grass ley came from carbohydrate, and the energy composition was similar between habitat types and seasons (9 ± 5 % fat, 16 ± 4 % protein, 74 ±5 % carbohydrate). In comparison, the composition of the energy in cereal and non-cereal crops varied with season; fat made

up over four times the proportion of energy shown above in cereal during winter and in non-cereal during winter and spring (Figure 4.3). The high fat content of forage within these habitats, which were not selected by hares, is illustrated in Figure 4.2. Protein made up 47% of the energy in cereal during the autumn, and 37% of energy in non-cereal during summer (Figure 4.3). Cereal and non-cereal were avoided in autumn and summer respectively (Table 4.2).

Table 4.2 Habitats ranked in order of energy and fat content (highest value first) for each season, along with the rank order of habitat use (1 = most used). Habitats that were utilised > 5% more (select) or less (avoid) than the % availability of the habitat at the site are indicated.

Season	Habitats ranked for energy content	Selection rank	Habitats ranked for fat content	Selection rank
Spring	Non-cereal	3	Non-cereal	3
	Grass ley	5	Ley grass	5
	Fallow land	1.5	Pasture	1.5 (select)
	Cereal	4	Fallow land	1.5
	Pasture	1.5 (select)	Cereal	4
Summer	Pasture	1.5 (select)	Ley grass	4
	Fallow land	1.5	Pasture	1.5 (select)
	Cereal	3	Fallow land	1.5
	Non-cereal	5 (avoid)	Non-cereal	5 (avoid)
	Grass ley	4	Cereal	3
Autumn	Fallow land	2	Cereal	4 (avoid)
	Cereal	4 (avoid)	Pasture	1
	Pasture	1	Fallow land	2
	Grass ley	3 (select)	Ley grass	3 (select)
	Non-cereal	5	Non-cereal	5
Winter	Grass ley	1	Cereal	5
	Non-cereal	4	Non-cereal	4
	Cereal	5	Ley grass	1
	Pasture	2	Pasture	2
	Fallow land	3	Fallow land	3

Figure 4.3 Energy composition of i) cereal and ii) non-cereal habitat, in terms of % fat, protein and carbohydrate, in relation to season. Missing data indicates a non-sampled season.

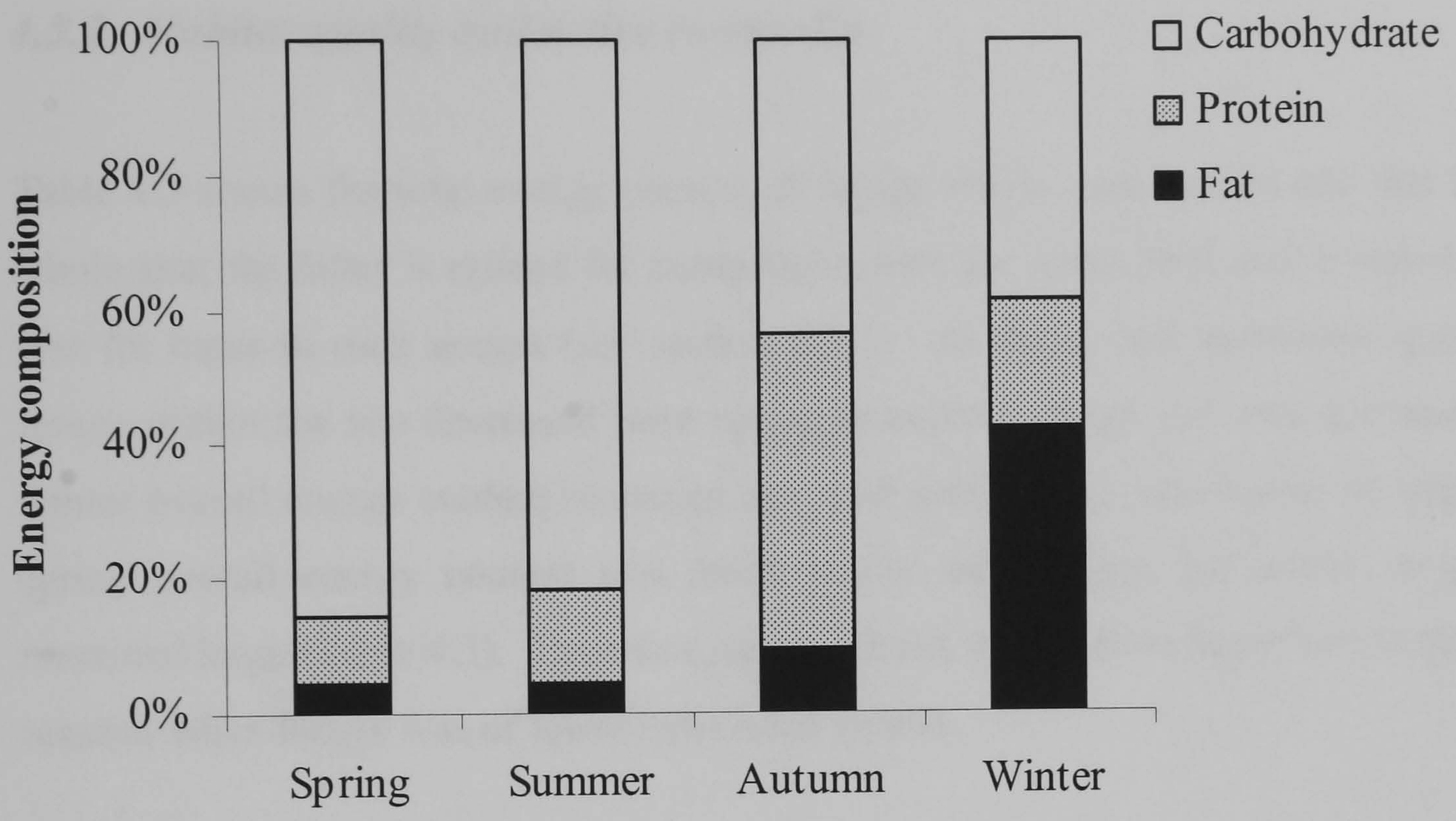

Figure 4.3.1

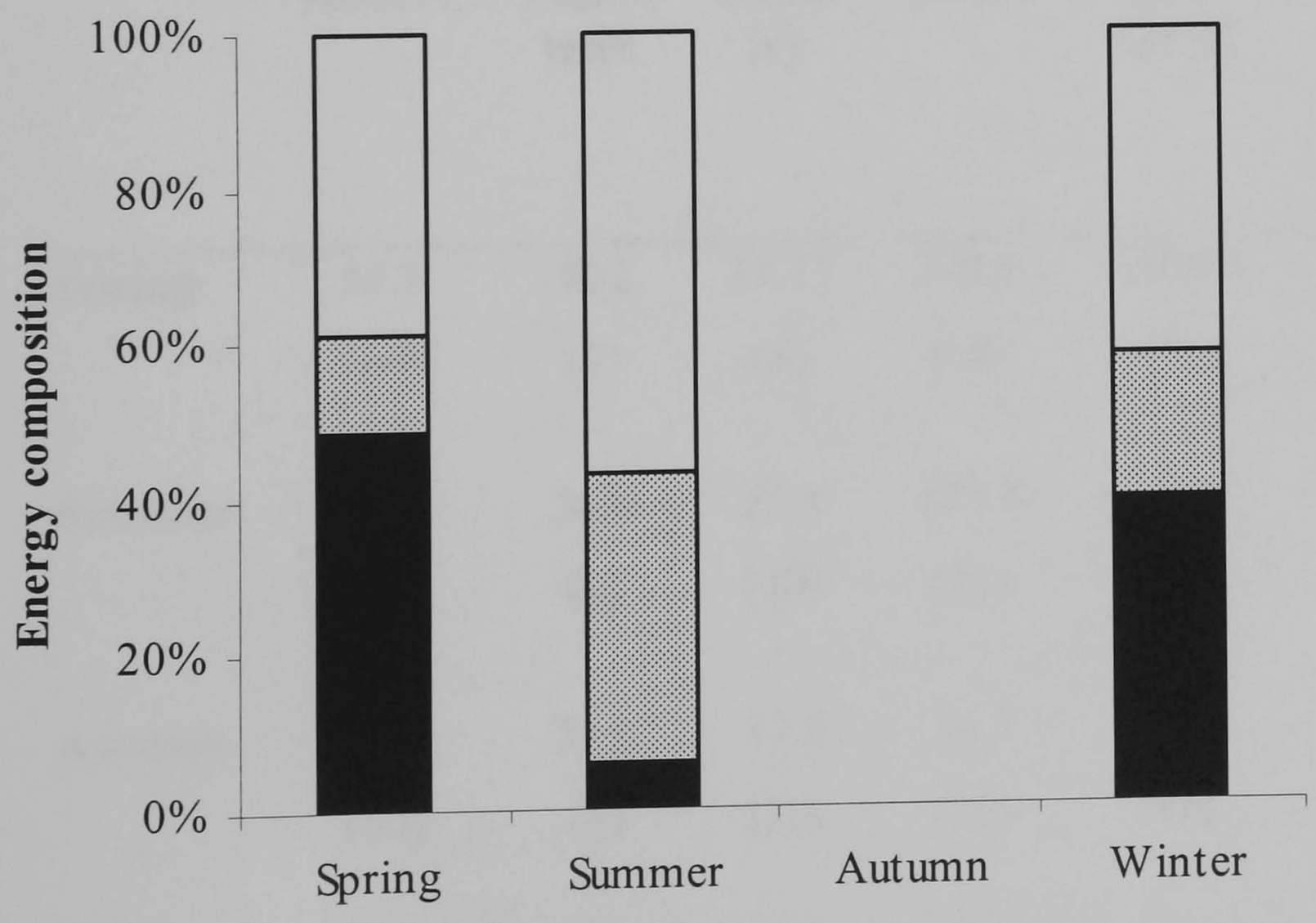

Figure 4.3.2

Results suggest that whilst there was some selection for high quality habitats in summer and winter, hares did not tend to select habitats based on forage quality.

4.3.2 Habitat quality and active range size

Table 4.3 shows the total energy content of forage within each habitat and that for the whole site; the latter is ranked for comparison with the mean 95% active kernel range size for hares in each season (see section *3.3.1*). As the overall nutritional quality of forage within the site decreased from spring to autumn, range size also decreased. In winter overall energy content remained low, and active range size was at its largest; in spring overall energy content was much higher than winter, but active range size remained large (Table 4.3). Therefore, hares did not tend to have larger active ranges in seasons when forage was of lower nutritional quality.

Table 4.3. Mean energy content (kJ) per unit area of each habitat type, total energy content of the whole study site (shown in parentheses next to the rank; 1 = largest value), and 95% active kernel range sizes. The availability (% of area) of each habitat type at the study site is shown in parentheses. † = calculated as a mean of the seasons either side.

	Pasture	**Fallow land**	**Grass ley**	**Cereal**	**Non-cereal**	**Whole site ranked (million kJ)**	**Active range size ranked (ha)**
Spring	34.3 (60)	30.2 (6)	31.1† (8)	293.9 (10)	1007.4 (11)	1 (83139)	36.6
Summer	42.7 (60)	36.8 (8)	33.4 (10)	125.4 (11)	14.3 (7)	2 (23599)	24.8
Autumn	21.9 (60)	21.6 (8)	13.5 (10)	16.7 (15)	0.0 (2)	4 (9618)	21.2
Winter	17.4 (60)	9.9 (6)	28.8 (8)	22.5 (10)	32.9 (11)	3 (9622)	64.3

4.4 Discussion

4.4.1 Quality of habitats selected

My data showed that the nutritional quality of forage within some habitats changed with season; grass ley and arable crops (cereal and non-cereal) had a higher energy and fat content in winter, and also in spring for non-cereal crops, than at other times of year (Figures 4.1 and 4.2). Most arable crops and grass ley are sown in the autumn, and so in winter they have recently emerged and are at their most digestible, containing less fibre than at later stages of development (McDonald *et al.* 1995). Hares in mixed and arable landscapes feed on crops at this time of year in particular (Frylestam 1986; Tapper & Barnes 1986; Chapuis 1990). At my pastural site, cereal and non-cereal crops were not selected in either winter or spring. Therefore, hares did not select habitats of high nutritional quality over those of low quality for foraging during these seasons. Mountain hares *Lepus timidus* show no preference for plant species of high nutritional quality; even in winter most plant species supply enough important nutrients, provided that energy demands are met (Pehrson 1984). In addition, hares practice caecotrophy: plant materials are separated into less digestible material, which is excreted, and fine materials high in nutritive value, which are reingested. This efficient breakdown of plant matter enables hares to live on low quality plant parts such as twigs over winter (Pehrson 1984; Homolka 1987b).

In summer there was some selection for habitats containing high quality forage, although there were only small differences in nutritional quality. If forage within all habitats was of low quality during the summer, as suggested by studies in arable landscapes (Frylestam 1980a, 1986; McLaren 1996), small differences in nutritional quality may have been important to hares. However, my data show that in summer the overall energy content of forage within the site was two and a half times that in autumn and winter (Table 4.3). Therefore, unlike populations of hares in arable landscapes, the population at my pastural study site was not limited by forage quality in summer.

Hares did not tend to select habitats containing forage of high nutritional quality over those of low nutritional quality through the year. The quality of pasture changed little with season, suggesting that this habitat type is fairly stable in terms of nutritional quality. Energy and fat content were highest in pasture in winter, when hares may have

been forage-limited due to low levels of vegetative growth. Hares did not select arable crops over pasture, even when the quality of forage within arable habitats was much higher.

4.4.2 Habitat quality and active range size

Seasonal differences in active range size were not explained by overall nutritional quality at the site. My data did not support the view that mammals in areas of low forage quality have larger ranges than those in areas of high forage quality (Harestad & Bunnell 1979). Instead, as the overall energy content of forage within the site decreased, active range size also decreased from spring to autumn (Table 4.3). However, neither was the availability of energy a constraint to range size (Swihart 1986) because in winter, when the overall forage quality of the site was low, hares had the largest active range size.

A possible explanation for the small active range size in autumn, when overall forage quality was low, is that there was no apparent nutritional advantage to increasing range size to include particular habitats for foraging, as they were all of similar quality. In winter, energy demands are high as it is the start of the breeding season and air temperatures are low (Myrcha 1968; Hackländer *et al.* 2002b). Therefore, it would seem advantageous for hares to increase active range size to include habitats of high nutritional quality at this time of year. However, cereal and non-cereal crops were not selected, and although grass ley was selected (Table 4.2), 40% of animals had none within their active range. In spring, range size remained high, even although the overall energy content of forage within the site was very high and hares selected pasture, which was readily available at the site. Changes in forage quality do not explain seasonal variations in range size, but changes in the quality of cover or behavioural changes related to breeding may (see Chapter 3).

4.4.3 Conclusions

Hares in pastural landscapes are present at relatively low numbers (Hutchings & Harris 1996; see Chapter 2), are in poor condition (Frylestam 1980b; Appendix 2) and are less likely to participate in breeding than hares in arable landscapes (Appendix 2). This is not due to diet quality (Appendix 2) or due to the lack of high quality habitats in terms of forage. Hares in pastural landscapes have smaller home ranges than those in arable landscapes (see Chapter 3) although they are able to cover relatively large ranges when forage quality is low. The only season in which hare populations may be limited by forage quality in pastural landscapes is autumn. Although energy demands are lowest during this season, as it is the non-breeding season (Raczyński 1964; Lincoln 1974; Hansen 1992), hares build up their fat deposits during the autumn. Low forage quality in pastural landscapes during the autumn may account for hares having low levels of kidney fat in these areas. In arable landscapes hares have higher levels of kidney fat (Appendix 2), which may reflect higher forage quality in the autumn. However, the nutrient quality of pasture is fairly stable through the year (Figures 4.1 and 4.2), and the quality of the diet of a grazing animal is always higher than the mean quality of forage within the habitat because of selection: hares not only select specific species of plants, but also particular plant parts (Brüll 1976; Homolka 1987b). Therefore, hare populations in pastural landscapes are not limited by habitat in terms of forage quality, but in terms of cover (see Chapter 3).

In the next chapter I compare population growth rates in arable and pastural landscapes, and investigate which demographic parameters have the greatest effect on population growth.

Chapter 5

Modelling demographic processes in high- and low-density populations of European hares

A manuscript based on this chapter has been submitted to *Biological Conservation*:

Smith, R.K., Jennings, N.V., Baker, P.J. & Harris, S. Modelling demographic processes in high- and low-density populations: can the decline of European hares *Lepus europaeus* be reversed?

Modelling demographic processes in high- and low-density populations of European hares

5.0 Summary

I used matrix models based on parameters derived from hare carcasses, the radio-tracking study (Chapter 3) and the literature to identify how demographic parameters drive hare population numbers, and why pastural landscapes support lower numbers of hares than arable landscapes. I also determined the magnitude of parameter changes required to produce positive population growth rates, and the time it would take to double hare population numbers. Population modelling indicated that growth rates were most sensitive to adult survival rates. In pastural landscapes, populations were declining, whereas those in arable landscapes were stable or increasing. Recruitment rather than adult survival is thought to limit pastural populations, as fecundity and juvenile survival rates were lower than in arable landscapes. Large parameter increases were required to produce population growth in pastural landscapes. I identified the need for additional data on population demographics, particularly from pastural landscapes.

5.1 Introduction

The objective of the UK European hare BAP is to double spring numbers in Britain by 2010 (Anonymous 1995), and it is believed that management for this increase in numbers should be focused in pastural landscapes (McLaren *et al.* 1997). To enable sound habitat management decisions to be made, it is important to understand how changes in habitats affect the population dynamics of species. However, as I highlighted in Chapter 2, little work has been done to quantify the effects of changes in agricultural habitats on hare numbers or demographic parameters, or to identify why numbers are lower in pastural landscapes.

Pastural landscapes appear to be suboptimal for the species; hares in mainly pastural areas in Sweden have higher mortality rates and lower body weight than those in more diverse mixed landscapes, and hares of lower body weights produce smaller litters (Frylestam 1980b). The proportion of females lactating is also lower in pastural landscapes than in arable landscapes (Appendix 2). Therefore both survival and recruitment may be lower in pastural landscapes than in arable areas. Life-history theory suggests that populations of short-lived species are likely to be limited by recruitment, whereas those of long-lived species are more sensitive to adult survival (Read & Harvey 1989). Hare populations may be sensitive to both elements; their position along the continuum may be dependent on the age structure of the population (Marboutin & Péroux 1995). For example decreasing populations may be more sensitive to adult survival than to recruitment (Marboutin & Péroux 1995). Therefore, to understand how changes in agricultural habitats affect hare populations, we need to determine how changes in demographic parameters affect population growth in different habitats.

In this chapter, I derive age-structured, density-independent, time-invariant matrix models based on demographic parameters obtained from hare carcasses from high- and low-density populations, from the radio-tracking study (Chapter 3), and from the literature. I aim to explain why pastural landscapes support fewer hares than arable landscapes in terms of population dynamics, and how demographic parameters affect population growth. I also determine the magnitude of parameter changes required to produce positive population growth rates and the number of years it would take to

double population sizes, and indicate how future research on demographic parameters and conservation measures should be targeted. To achieve these aims I i) compare population parameters and mean life span of hares in different landscapes, ii) use matrix models to simulate and compare population growth rates in arable and pastural landscapes, iii) carry out sensitivity analysis to identify which parameters have the greatest effect on population growth rates, and iv) determine the magnitude of parameter changes required to achieve positive population growth rates, and the time taken to double model population numbers.

5.2 Methods

5.2.1 Carcass collection

Data on fecundity (proportion breeding x litter size) and survival were obtained from the post mortem examination of 920 carcasses collected between 1998 and 2001, from 128 locations in England and Wales: 774 from 28 shooting estates and the remainder mainly killed on roads. Here I use data from carcasses from the three 'landscape types', arable *a*, arable *b* and pasture, based on a combination of division 3 and 4 aggregations of the Institute of Terrestrial Ecology's land class database (now Centre for Ecology and Hydrology; Bunce *et al.* 1996). Arable *a* and arable *b* landscapes are very similar in land use and geology, but arable *a* occurs in southern England, and arable *b* in eastern and central England (Bunce *et al.* 1996). Average hare densities in the 1990s were: 3.3 hares 100 ha^{-1} in arable *a*, 9.0 hares 100 ha^{-1} in arable *b* and 3.0 hares 100 ha^{-1} in pastural landscapes (Hutchings & Harris 1996).

5.2.2 Age determination

The age of each animal was determined by using a combination of three independent methods: eye lens weight (Suchentrunk, Willing & Hartl 1991), analysis of adhesion (growth) lines in periosteal tissue in the jaw bone (Frylestam & Schantz 1977; Pascal & Kovacs 1983), and the presence or absence of an epiphyseal protrusion of the lateral

ulnar knob (Stroh 1931; for further details see Appendix 2). At least one of the most robust methods (eye lens weight or adhesion lines in mandibles) was used for 97% of carcasses. When more than one method was used, results were always consistent. Each hare was placed in one of the following age classes: subadult (4 - 7.7 months), young adult (7.7 - 12 months), adult (> 12 months). Leverets and juveniles (0 - 3 months) were not represented in the carcass sample. For the construction of a seasonal model, young adults were split into two age classes: young adult 1 (7 - 9 months) and young adult 2 (10 - 12 months). Survival and fecundity data for young adult classes 1 and 2 were assumed to be equal; annual survival and fecundity for adults were considered to be independent of age (Broekhuizen 1979).

5.2.3 Breeding status and fecundity

The carcasses of 422 female hares were obtained from arable *a* (25%), arable *b* (65%), and pastural (10%) landscapes. Since hares are rarely shot except in February in England and Wales, data on breeding status and fecundity were only available for the winter season, from 356 females. Seasons were defined as: spring = 22 March – 21 June, summer = 22 June – 23 September, autumn = 24 September – 21 December, and winter = 22 December – 21 March. Females were classed as pregnant (viable or resorbing embryos visible to the naked eye), lactating (milk extrusion from mammary tissue) or not breeding. Since milk is present in the mammary glands of rabbits in the last few days of pregnancy (Brambell 1942), females were not classed as lactating if they carried embryos that were near full-term (≥38 days since conception). Viable embryos were counted and aged to the nearest day of gestation based on their body weight (Broekhuizen & Martinet 1979) so that the season of birth could be estimated.

Uteri of non-pregnant females were examined for recent uterine scars (Bray 1998; Appendix 2). Scars classed as < 48 days old were used to determine the current litter size (Bray 1998). From these scars, the season of birth was calculated for currently nursing litters by assuming they had been born 15 days before (i.e. were half-way through the nursing period; Broekhuizen & Maaskamp 1980). In females that were pregnant and lactating, the season of birth was calculated only from pregnancy since

this was more accurate. Resorbing embryos, which constituted 13% of all those examined, were not included in estimates of litter size.

Fecundity rates in winter

Age-specific fecundity rates in winter were estimated from the proportion of females killed in winter that were pregnant and the average size of litters due or born in winter. In rabbits, blastocysts are undetectable macroscopically for the first three days (10%) of the gestation period (Brambell 1942; Smith & Trout 1994). Assuming that early pregnancy is similar in hares I multiplied the proportion of females pregnant by 1.1. Average litter sizes were halved assuming a 1:1 sex ratio at birth (Raczyński 1964) as populations were projected using single-sex models. Leverets and juveniles were assumed not to breed. Hares can reach sexual maturity at the age of 4 months, but most become sexually active at 6 - 7 months (Broekhuizen & Maaskamp 1981). A large proportion of subadults sampled in winter were aged 6 - 7 months and had therefore been born towards the end of the previous breeding season (e.g. Lincoln 1974; Hansen 1992). So that fecundity data were not biased towards the productivity of these older subadults I determined the proportion of 4, 5, 6 and 7 month old subadults pregnant, and then calculated a mean for the age class.

Although females can be pregnant and lactating simultaneously, few females breed more than three times each year, and the average number of litters produced per year by each female in mixed agricultural landscapes is 2.3 (Hansen 1992) - 2.9 (Frylestam 1980c). Therefore, for modelling purposes I assumed that each female bred once in each season, except autumn when I assumed there was no breeding (Raczyński 1964; Lincoln 1974; Broekhuizen & Maaskamp 1981; Hansen 1992).

Fecundity rates in spring, summer, and autumn

To estimate fecundity rates for spring and summer, I extrapolated the winter fecundity values, based on the seasonal pattern observed in studies in which larger sample sizes were obtained in all seasons (Table 5.1). I applied average conversion values consistently in all age classes, across all landscapes, and assumed fecundity rate was zero in autumn (Raczyński 1964; Lincoln 1974; Broekhuizen & Maaskamp 1981).

Table 5.1 Seasonal fecundity rates (proportion breeding x litter size) obtained from the literature. The ratio of spring, summer and autumn rates relative to the winter rate are shown in parentheses. The average conversion values were used to extrapolate data for winter to the other seasons, except for autumn when I assumed that there were no births

Season	Raczyński (1964)	Lincoln (1974)	Hewson & Taylor (1975)	Broekhuizen & Maaskamp (1981)	Mean ratio relative to winter
Winter	0.47 (1.00)	0.46 (1.00)	0.58 (1.00)	0.79 (1.00)	1.00
Spring	1.24 (2.61)	1.73 (3.79)	1.36 (2.34)	1.41 (1.78)	2.63
Summer	0.84 (1.77)	0.40 (0.88)	0.72 (1.24)	0.74 (0.94)	1.21
Autumn	0.00 (0.00)	0.00 (0.00)	0.14 (0.24)	0.00 (0.0)	0.06

5.2.4 Survival

Subadult and adult survival from carcasses

Survival rates of hares in arable landscapes were calculated from the age structure of hares shot in February, assuming that hares in all age classes are equally likely to be shot (Broekhuizen 1979). This method could not be used for pastural landscape as hares are not shot in large numbers in these areas. Hare carcasses from shooting estates within a 50 km^2 area were assumed to come from the same population. Both male and female carcasses were included as there was no difference in the number of males and females shot from each age class in either landscape (arable *a*: $\chi^2 = 0.318$, $df = 2$, $P = 0.853$, $n = 130$; arable *b*: $\chi^2 = 4.567$, $df = 2$, $P = 0.102$, $n = 93$). Numbers of hares in each age class shot were used to construct life tables; all age classes < 1 year were combined. Annual finite survival rates were calculated: finite survival rate = N_t / N_0, where N_0 is the number of individuals alive at the start of the time period, N_t the number alive at the end, and t represents time (Krebs 1989). Mean adult survival rate was calculated from all adult age classes.

As leverets and juveniles are not present in the population in February (Lincoln 1974; Hansen 1992), I assumed that the survival rate calculated for the first age category applied only to subadults and young adults. For projection modelling I assumed that the survival rate of the two age classes was equal and converted the overall value for survival from 4 - 12 months to age-specific values using the duration of each age class as follows (Krebs 1989):

Instantaneous mortality rate (IMR) = ln (finite survival rate)

Adjusted instantaneous mortality rate (AIMR) = IMR x (t_s/t_o)

where t_s is the standardised time interval, the duration of each age class in days, and t_o is the observed time interval, 274 days.

Finite mortality rate (FMR) = $1.0 - e^{AIMR}$

Finite survival rate = 1.0 - FMR

Survival data from radio-tracking

Data on survival of hares in pastural landscapes were obtained by radio-tracking 16 leverets and juveniles, 30 subadults and 51 adults at the study area described in Chapter 3 (section *3.2.1*).

Juvenile, subadult and adult hares were captured using static nets and cage traps (for further details see section *3.2.2*). Leverets were found by making use of their nursing behaviour (Broekhuizen & Maaskamp 1980; Holley 1992). I searched for females and leverets from sunset for approximately two hours with the aid of a spotlight, and followed radio-collared females on successive nights; if they returned to the same place each night at a similar time I searched for leverets. I also searched for leverets in their form by using a thermal sensing device ('Infrarot-Wildretter'; Industrieelektronik GmbH, Weiden, Germany). This equipment was used at night when the ambient temperature was lower than the surface temperature of a leveret. Leverets were captured in a hand-held fishing net (75 cm diameter Powerspoon Maxicarp; Keenet, Romford, UK). One leveret was caught per 22 search hours.

Each hare was sexed and fitted with two ear tags and a radio collar (Supersmall tags, Dalton; Televilt, Lindesberg, Sweden; for further details see section *3.2.2*). Individual hares were placed in an age class based on the ageing methods described in Chapter 3 (section *3.2.2*) and on behavioural observations (whether still nursing or not). Hares were allocated to successive classes as they aged, based either on age at re-capture, or by assuming they were at the midpoint of the age range of their initial age class. Leverets and juveniles could not be sexed reliably and so sexes were pooled, as were these two age groups, which are referred to as juveniles for the remainder of the chapter.

Subadult and adult hares were located at least once each week. Those dying in the first week after capture were not used for survival estimates (Pollock *et al.* 1989). Juveniles were located every two days, and deaths were included even if they occurred

soon after release, since survival in juveniles is not significantly reduced during the first six days after release (Marboutin *et al.* 1990). Survival of littermates of tracked leverets that could not be captured was estimated by observation at the nursing site. These individuals were considered 'censored' once weaning had taken place. Using survival data from non-independent littermates does not bias the results, but reduces the variance in estimates of survival (Pollock *et al.* 1989). Hares not located for > 30 days were considered censored as of the last census date. When a fresh and intact carcass was found, death was considered to have occurred the previous day.

I used non-parametric analysis for right-censored data to derive a Kaplan-Meier survival function (Altman 1991; Release 13.31, Minitab software, UK). This method allows animals to be added to the sample throughout the study and for animals to be censored (Pollock *et al.* 1989). From the function I estimated survival probabilities and 95% confidence intervals for annual survival for adults, and for survival over the maximum duration of each age class for younger animals. The same survival function was used for adults and young adults, as these age classes could not be distinguished on capture.

Seasonal survival rates and mean life span

For model matrices, survival values for the duration of each age class (finite survival rates) were converted to survival probabilities for standard 91-day seasons, using the equations in section *5.2.4* (Krebs 1989). The standardised time interval was the duration of a season, and the observed time interval the duration of each age class.

I determined the mean life span from annual adult survival rates (S) as follows: mean life span = [1/(1-S)] + 0.5 (Marboutin & Péroux 1995).

5.2.5 Projection model

Population growth was extrapolated in each landscape using a simple one-sex, age-structured (5 age classes), density-independent, time-invariant matrix model (Leslie 1945; Caswell 2001); emigration and immigration rates were assumed to be equal. Models were created using spreadsheet software (Microsoft Excel) and were projected over a 20-year period. Each model comprised four matrices, corresponding to the four

seasons in each year; a combination of matrices allowed for breeding in a given year by animals born earlier in that year. Initial population size was set at 200 animals distributed in accordance with the stable age distribution. Matrices generated from the age-specific survival and fecundity data were used to generate stable age distributions, starting with a population of 1000 adults in winter. The final output of the models was annual population growth rate (λ), determined by comparing population size at the start of each successive winter; populations were stable when $\lambda = 1$, increasing when $\lambda > 1$ and declining when $\lambda < 1$. For the perturbation analysis, variables in the models were adjusted individually or in combination to i) determine the sensitivity of λ to parameter changes, ii) achieve a $\lambda > 1$, and iii) determine the number of years required to double population size.

5.3 Results

5.3.1 Fecundity

Winter fecundity rates for adults and young adults in arable *a* and arable *b* landscapes were similar, and higher than those in pastural landscapes, due to both higher proportions of pregnant females and larger litter sizes (Table 5.2). Subadult fecundity rates were higher in arable *a* than in arable *b* landscapes. Only one subadult was examined from pasture in winter, and so I used the value estimated for subadults in arable *b* landscapes for the pastural projection model. This value was used because the proportion of adults pregnant in pasture was lower than in both arable landscapes, and arable *b* had the lowest value for subadults (Table 5.2). As no young adults were examined from pasture, I assumed that the proportion of young adults pregnant was the same as for adults in this landscape (Table 5.2). Table 5.3 shows the fecundity rates extrapolated for spring, summer and autumn for the model matrices (extrapolated from Tables 5.1 and 5.2).

Table 5.2 Female fecundity rates (proportion breeding x litter size) in winter in three landscapes and four age classes. Proportion of females breeding calculated from carcasses, except † = estimated based on relationships between proportions of adults and other age classes breeding in arable landscapes. Also shown are estimated litter sizes (female offspring only; ‡ = assumed to be equal to litter size for adults). Sample sizes are shown in parentheses.

Age class	Arable *a*			Arable *b*			Pastural		
	Proportion pregnant	Litter size	Fecundity rate	Proportion pregnant	Litter size	Fecundity rate	Proportion pregnant	Litter size	Fecundity rate
Juvenile	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Subadult	0.79 (13)	0.60 (10)	0.48	0.51 (25)	0.54 (14)	0.27	0.51 †	0.50 ‡	0.25
Young adult	0.87 (24)	0.56 (9)	0.48	0.84 (34)	0.58 (25)	0.49	0.64 †	0.50 ‡	0.32
Adult	0.74 (58)	0.67 (27)	0.49	0.73 (167)	0.59 (90)	0.43	0.64 (12)	0.50 (3)	0.32

Table 5.3 Extrapolated female fecundity rates for spring, summer and autumn.

Age class	Arable *a*			Arable *b*			Pastural		
	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
Juvenile	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Subadult	1.25	0.58	0.00	0.71	0.33	0.00	0.67	0.31	0.00
Young adult	1.27	0.58	0.00	1.28	0.59	0.00	0.84	0.39	0.00
Adult	1.29	0.60	0.00	1.14	0.52	0.00	0.84	0.39	0.00

5.3.2 Survival

There was no significant difference between survival probabilities of males and females in the subadult (log-rank = 0.858, $df = 1$, $P = 0.354$, $n = 21$ females and 9 males) or adult age class (log-rank = 3.607, $df = 1$, $P = 0.058$, $n = 30$ females and 21 males; Pollock *et al.* 1989) in the pastural landscape.

Of the sample of 16 juveniles (from nine different litters), only three were monitored for more than 34 days, and all of these were censored (at 89, 133 and 196 days). Therefore, I was unable to calculate survival probabilities for the juvenile age class, which lasts 122 days. Survival probability after 34 days was 0.40 (lower-upper 95% CIs: 0.07 - 0.73); survival over 122 days was therefore much lower. In Europe, survival of young between birth and the shooting season in September – December was 0.23 - 0.50 (Pépin 1989) and 0.53 (Frylestam 1980c) in arable areas, 0.26 (range 0.19 - 0.32; Hansen 1992) and 0.23 (Frylestam 1980c) in mixed areas, and 0.18 in a mainly pastural area (Frylestam 1980c). Survival of leverets was 0.20 (range 0.14 - 0.25) in an arable area and 0.29 in a mixed area (Marboutin *et al.* 2003). I used approximate survival values of 0.3 for arable landscapes and 0.2 for pastural landscapes for the juvenile age class.

Survival rates for adults were similar in the three landscapes (Table 5.4). Those for subadults and young adults were similar in the two arable landscapes but lower than in pastural landscapes (Table 5.4). The mean life span for hares in each landscape was 2.7 years for arable *a*, 2.5 years for arable *b* and 2.5 years for pastural landscapes.

5.3.3 Projection model

The default annual population growth rates (λ) using the stable age distributions generated (Table 5.5) were 1.08 for arable *a*, 0.99 for arable *b*, and 0.84 for pastural. Therefore, based on the initial starting values, model populations in arable *a* landscape are predicted to grow, those in arable *b* landscape are approximately stable, while populations in pastural landscapes decline.

Table 5.4 Estimates of survival probabilities of female hares for the duration of each age class, and standardised for 91-day seasons. Sources of data: † = Frylestam 1980b, Pépin 1989, Hansen 1992 and Marboutin *et al.* 2003, data from hunting bags and placental scars, ‡ = carcasses from British shooting estates collected for this study, § = radio-tracking data collected in this study; lower and upper 95% confidence intervals are shown in parentheses.

Age class (duration of class)	**Arable *a***		**Arable *b***		**Pastural**	
	Duration of class	**91-day season**	**Duration of class**	**91-day season**	**Duration of class**	**91-day season**
Juvenile (122 days)	0.30 †	0.407	0.30 †	0.407	0.20 †	0.301
Subadult (113 days)	0.69 ‡	0.740	0.70 ‡	0.750	0.76(0.58, 0.94) §	0.802
Young adult (131 days)	0.65 ‡	0.740	0.66 ‡	0.750	0.79(0.67, 0.90) §	0.849
Adult (365 days)	0.55 ‡	0.860	0.50 ‡	0.842	0.51(0.33, 0.69) §	0.845

In perturbation analysis, I increased the age-specific seasonal survival and fecundity parameters individually by 5% to determine the sensitivity of λ to these changes (Table 5.6). I also considered 5% year-round increases in the parameters (in all four seasons concurrently; Table 5.7). In all models, λ was more sensitive to changes in survival than to changes in fecundity, and much more sensitive to changes in adult survival than to changes in survival of any other age class (Tables 5.6 and 5.7, Figure 5.1). A 5% increase in adult survival year-round resulted in a 9 - 11% increase in λ, whereas a similar increase in adult fecundity only resulted in a 1 - 2 % increase in λ (Table 5.7). Apart from adult survival, λ was most sensitive to juvenile survival. Survival rates had a greater effect on λ than fecundity for all age classes.

Table 5.5 Stable age distributions (proportions in each age class) used in the models for each landscape. No juveniles occur because there is no breeding in autumn and the starting point to generate the stable age population was winter.

Age class	Arable *a*	Arable *b*	Pastural
Juvenile	0.00	0.00	0.00
Subadult	0.19	0.16	0.11
Young adult 1	0.28	0.29	0.20
Young adult 2	0.10	0.10	0.08
Adult	0.43	0.45	0.61

Model populations in pastural landscape remained in decline ($\lambda < 1$) when parameters were increased by 5% (Table 5.6 and 5.7). To determine the magnitude of parameter increases required to obtain a value > 1 for λ, I increased age-specific survival and fecundity parameters individually by further 5% increments year-round (10%, 15%, …, *n*%) for the age classes that had the greatest effect on λ (see Table 5.6). A $\lambda > 1$ was achieved by increasing adult survival by 10% ($\lambda = 1.05$), juvenile survival by 55% ($\lambda = 1.03$) or adult fecundity by 85% ($\lambda = 1.04$; Figure 5.1). I then increased age-specific survival in combination, by 5% increments year-round, starting with juveniles and then increasing survival of an additional subsequent age class. A 15% increase in all age classes < 1 year was required to achieve a $\lambda > 1$ ($\lambda = 1.04$). To determine whether smaller increases in parameters were required if survival and

Table 5.6 Annual population growth rate and in parentheses its sensitivity (% change from default value) to 5% increases in each parameter individually. No change (including changes of < 1%) are indicated as - ; age classes for which all changes were < 1% are not shown.

Parameter	Age class	Season	Arable *a*	Arable *b*	Pastural
Fecundity	**Young adult 2**	Winter	-	-	-
		Spring	-	1.00 (1)	-
		Summer	-	-	-
		Autumn	-	-	-
	Adult	Winter	-	-	-
		Spring	-	1.00 (1)	-
		Summer	-	1.00 (1)	-
		Autumn	-	-	-
Survival	**Juvenile**	Winter	-	-	-
		Spring	-	1.00 (1)	-
		Summer	1.09 (1)	1.01 (2)	-
		Autumn	1.09 (1)	1.00 (1)	-
	Subadult	Winter	-	1.00 (1)	-
		Spring	-	-	-
		Summer	-	1.00 (1)	-
		Autumn	1.09 (1)	1.01 (2)	-
	Young adult 1	Winter	1.09 (1)	1.00 (1)	-
		Spring	-	1.00 (1)	-
		Summer	-	-	-
		Autumn	-	1.00 (1)	-
	Young adult 2	Winter	-	1.00 (1)	-
		Spring	1.09 (1)	1.00 (1)	-
		Summer	-	-	-
		Autumn	-	-	-
	Adult	Winter	1.10 (2)	1.01 (2)	0.86 (2)
		Spring	1.10 (2)	1.01 (2)	0.86 (2)
		Summer	1.10 (2)	1.01 (2)	0.86 (2)
		Autumn	1.10 (2)	1.02 (3)	0.86 (2)

Table 5.7 Annual population growth rate and in parentheses its sensitivity (% change from default value) to 5% increases (year-round) in each parameter. No change (including changes of < 1%) is indicated by -.

Parameter	Age class	Arable *a*	Arable *b*	Pastural
Fecundity	**Subadult**	-	-	-
	Young adult 1	-	1.00 (1)	-
	Young adult 2	-	1.00 (1)	-
	Adult	1.09 (1)	1.01 (2)	0.85 (1)
Survival	**Juvenile**	1.11 (3)	1.02 (3)	0.85 (1)
	Subadult	1.10 (2)	1.02 (3)	0.85 (1)
	Young adult 1	1.10 (2)	1.01 (2)	0.85 (1)
	Young adult 2	1.09 (1)	1.01 (2)	0.85 (1)
	Adult	1.18 (9)	1.08 (9)	0.94 (11)

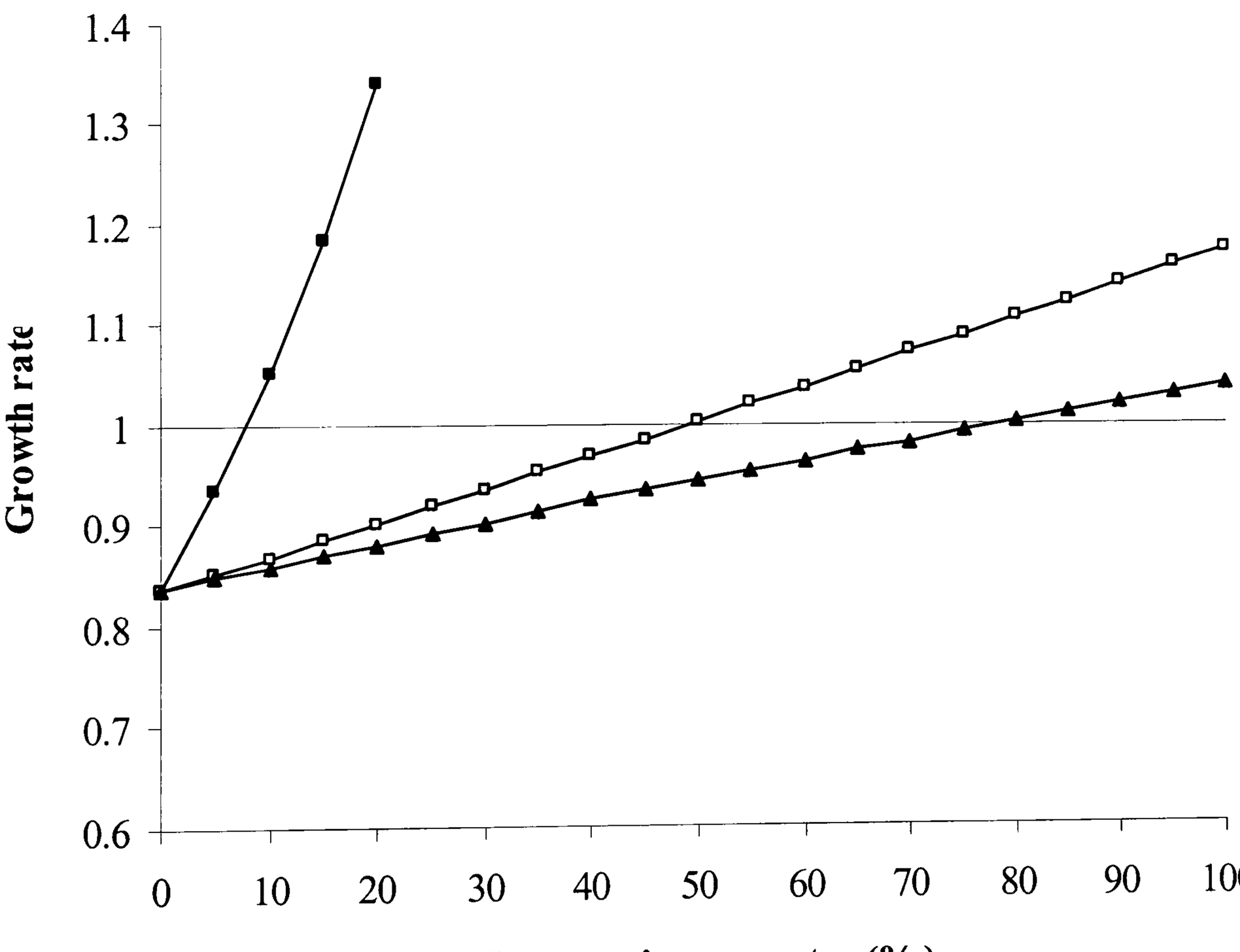

Figure 5.1 Sensitivity of the pastural model population growth rate to increases in adult (■) and juvenile (□) survival rate, and adult fecundity (▲).

fecundity were increased in combination, I increased adult parameters together as they had the greatest effect on λ. An increase of 5% in fecundity and 10% in survival, or an increase of 35% in fecundity and 5% in survival, were needed to produce a $\lambda > 1$ (λ = 1.07 and 1.05 respectively).

When adult survival was increased by 10% year-round (λ = 1.05), the model pastural population doubled in 15 years; for all other parameter increases modelled it took 20 or more years for the population to double. In comparison, the arable *a* population doubled in 10 years at the default λ, and the model arable *b* population doubled over the same time period if adult survival was increased by 5% year-round.

5.4 Discussion

5.4.1 Life span and population parameters in different landscapes

Mean life span of hares in the pastural landscape was the same as in arable *b* landscapes (2.5 years), and similar to that in arable *a* landscapes (2.7 years). These figures are similar to those in the literature (e.g. 2.9, 2.0, 2.2 and 2.5 years; Abildgård *et al.* 1972; Broekhuizen 1979; Pépin 1987; Marboutin & Péroux 1995 respectively).

Adult fecundity rates in pastural landscapes were 53% and 34% lower than in arable *a* and arable *b* landscapes respectively. The fecundity rates for arable landscapes were similar to those of other arable populations (Raczyński 1964; Lincoln 1974; Table 5.1 and 5.2). Fecundity in pastural landscapes was estimated based on a small sample size, although Frylestam (1980c) also found that mean litter size was lower in a pastural landscape than in mixed or arable landscapes. Female reproductive success is correlated with body size and weight (Frylestam 1980c), and since hares in pasture are smaller and weigh less than those in arable habitats (Frylestam 1980c; Appendix 2), the fecundity rates calculated are realistic.

5.4.2 Population growth rates in different landscapes

Model arable populations reached stable age distributions similar to those observed in real winter populations (% of population < 9 months old: model arable *a* 47%, arable *b* 45%; real populations 43% Jezierski 1968; 55%, Bresinski 1983). This suggests that the projection models provide useful, although simplified, information about population dynamics in wild populations. The model pastural population had a lower proportion of young (39%) than arable populations. Comparable data for this landscape are not available for winter, but in autumn 53% of a pastural population are young individuals (Frylestam 1979). The fact that this is higher than the value I calculated is not surprising as autumn is the end of the breeding season; the proportion of young is also higher in arable landscapes in autumn (68%, Pepin 1978; 70%, Frylestam 1979; 59%, Marboutin & Péroux 1995) than in winter.

Results suggested that the model population in arable *a* landscape was increasing, while that in arable *b* was approximately stable. The model for pastural landscapes predicted that populations were declining. These results are similar to trends in real populations. Populations of hares declined in all landscapes throughout Britain between 1960 and 1980 (Tapper 1992). A questionnaire study in England and Wales found that although 42% of farmers described hare numbers as having decreased since 1980, 22% described them as having increased and 36% described them as stable (Vaughan *et al.* 2003). Arable farmers were the most likely to have experienced increases, and sheep farmers most likely to have experienced a decline (Vaughan *et al.* 2003). Hare numbers in pastural landscapes are lower than in arable landscapes and are more likely to have continued to decline since 1980 (Hutchings & Harris 1992; McLaren *et al.* 1997; Vaughan *et al.* 2003).

5.4.3 Effect of parameters on population growth rate

Although populations of lagomorphs may be sensitive to changes in recruitment (Read & Harvey 1989; McLaren *et al.* 1997), in all models λ was most sensitive to adult survival. The same applied to a declining population in France (Marboutin & Péroux 1995). However, the French population had a lower proportion of young, and therefore

lower recruitment, than typical hare populations; when the proportion of young was increased to 66%, λ was more sensitive to recruitment than to maintenance (Marboutin & Péroux 1995). All my model populations had < 66% young, and the declining pastural population had the lowest proportion. Pastural populations had lower fecundity and juvenile survival rates than arable landscapes, indicating that recruitment was low.

Results from model projections suggested that the most effective way to increase hare populations was to increase adult survival. It is unclear as to what the main causes of mortality in adult hares are; of the 81 subadult and adult hares I radio-tracked, 50 were known to have died, but the cause of death could be ascertained in only 7: 2 died from disease, 2 from traumatic injuries, and 3 were killed by poachers. Most carcasses had been either predated or eaten as carrion by foxes, but it was not possible to determine which. Although foxes take mostly leverets and few adults, predation by this species may limit populations of hares (Lindström *et al.* 1994; Reynolds & Tapper 1995; see Chapter 2). Adult survival could be increased by reducing hunting pressure, predation, or exposure to adverse weather conditions by providing vegetative cover (see Chapter 3). Although some data are available on the level of hunting pressure faced by populations of hares in arable landscapes in Britain (29 - 69% of individuals removed on driven shoots; Stoate & Tapper 1993), little is known about the level faced by populations in pastural landscapes. Hares are not shot on driven shoots as they are in arable landscapes, but some form of shooting takes place on 7% of pastural farms, compared to shoots on 11% of arable *a* and 16% of arable *b* farms (Vaughan *et al.* 2003; N. Vaughan Jennings, pers. comm.). Hares in both arable and pastural landscapes are hunted with dogs, in the form of coursing and beagling (for definitions see section *3.2.1*), and are subject to poaching on 9% of arable *a* farms, 11% of arable *b* farms, and 8% of pastural farms (Vaughan *et al.* 2003; N. Vaughan Jennings, pers. comm.).

5.4.4 Achieving a positive population growth rate in pastural landscapes

To achieve a positive growth rate in the model pastural population, seasonal adult survival rates needed to be increased by 10%, to a level equivalent to an annual adult survival rate of 0.75. This is much higher than in real populations (e.g. Frylestam 1979; Pépin 1987; Marboutin & Péroux 1995).

Although λ was most sensitive to adult survival rates, in pastural landscapes adult survival was similar to that in arable landscapes, whereas fecundity and juvenile survival rates were lower than in arable areas. Therefore it is likely that pastural populations are limited by recruitment, as suggested by McLaren *et al.* (1997). Results indicated that after adult survival, λ was most sensitive to the survival of juveniles. Recruitment may limit populations because of poor body condition in breeding individuals (Frylestam 1980c; Appendix 2), and low juvenile survival due to poor quality cover (see Chapter 3).

A positive growth rate in the model pastural population was achieved by increasing juvenile survival by 55%, which represents an increase from 0.20 to 0.36 for survival for the duration of the age class. This value is high for juveniles (Marboutin *et al.* 1990; Marboutin *et al.* 2003), and is more similar to the survival rate of subadults (Frylestam 1980c; Pépin 1987; Marboutin & Hansen 1998). However, few data are available on survival rates of juveniles in any landscape. As λ was less sensitive to fecundity than to survival it required an 85% increase in adult fecundity alone, or an increase in both adult fecundity and survival in pastural landscapes, to achieve a positive growth rate. These new parameter values are similar to or higher than those for arable landscapes.

5.4.5 Future conservation management and research

If small increases in population parameters are achieved in arable landscapes, hare populations could be doubled by 2010 to fulfil the UK Biodiversity Action Plan target. However, in pastural landscapes large increases in recruitment rate were required to produce a positive population growth rate, and so a doubling of the population is not possible over the same time scale. Results described in Chapter 3 and 4 suggest that increases in population parameters could be achieved by improving habitat quality in terms of cover in pastural landscapes (see Chapter 6).

By modelling hare populations in different landscapes I have achieved my aim of improving the understanding of how population parameters drive hare population numbers, and why pastural landscapes support low numbers of hares. However, more data are needed on fecundity in pastural landscapes, and on the survival of juveniles in

all landscapes. We also require a better understanding of the causes of mortality in older age classes.

In this chapter I have identified which population parameters have the greatest effect on hare population numbers, and which are most likely to limit hare populations in pastural landscapes. In the next chapter I bring together the main findings of this and previous chapters and discuss how future management and research should be targeted.

Chapter 6

Conclusions

Conclusions

6.1 Review of findings

To develop robust conservation management policies, it is vital to have a sound knowledge of the population dynamics of the target species. An understanding of how population numbers change with variations in each demographic parameter, and what factors are responsible for these variations is required. Factors that limit populations were discussed in Chapter 1, and in Chapter 2 I investigated which of these factors was most likely to have caused the decline in hare numbers throughout Europe. Hares are just one of the many mammalian species that are thought to have declined because of habitat changes caused by agricultural intensification, but little quantified evidence exists for the relationship between intensification and decline for any of these species (see section 1.3). Therefore, the hare, for which long-term data are available, is valuable as a study species, and findings for the hare may have important implications for the conservation of other species of farmland mammals. In addition, as the main objective of the UK European hare BAP is to increase numbers by the year 2010 (Anonymous 1995), there was some urgency to carry out research on the species to aid the development of effective habitat management plans.

Results in Chapter 2 indicated that habitat changes caused by the intensification of farming are the most likely cause for the decline of hare populations since the 1960s. The review highlighted the lack of data on habitat use and population demographics of hares in pastural landscapes. It also emphasised the need for an understanding of the actual mechanisms of the decline, i.e. which population parameters are most responsible for the changes in population size, and why numbers of hares are so low in pastural landscapes. In Chapters 3 and 4 I focused on two of these issues. I investigated habitat selection by hares in a pastural landscape to identify which habitat factors may limit populations in these landscapes. Results suggested that hare populations are not limited by habitats in terms of forage quality. However, hares select heterogeneous habitats

over homogeneous habitats, at the within-habitat scale in particular, and vary habitat selection with season. At my pastural study site, where hares are present at higher numbers than on average in pastural areas (Hutchings & Harris 1996), hares have access to heterogeneous habitats throughout the year as grazing management is not highly intensive. This, and the fact that hares have specific spatial and temporal habitat requirements, suggest that populations may be limited by habitat availability in terms of cover in pastural landscapes.

In Chapter 5 I focused on another of the subjects for which data were limited. I aimed to identify the demomographic mechanisms that cause the most significant changes in hare population numbers, and to explain why numbers are lower in pastural landscapes than arable landscapes. Although population size is most sensitive to changes in adult survival rates, populations in pastural landscapes are more likely to be limited by recruitment. Both fecundity and juvenile survival are lower in pastural areas than arable areas. Large increases in parameters are required to achieve population increases in pastural landscapes. Therefore I concluded that although populations in arable landscapes could be doubled by 2010 to achieve the UK Biodiversity Action Plan target, such increases would not be possible over the same time-scale in pastural landscapes.

In the following sections I outline the major changes in management of mixed, arable and pastural landscapes that resulted from agricultural intensification, and how these changes may have affected hare numbers. I focus on changes in management in Britain, but since agricultural intensity is high in all pre-2004 European Union countries because of legislation such as the Common Agricultural Policy (Bignal & McCraken 2000; Donald *et al.* 2002), changes in other European Union countries are likely to be similar. I also discuss how future management and research should be targeted in agricultural landscapes to increase numbers of hares, and assess whether it is feasible through habitat management, to maintain and expand existing hare populations in Britain.

6.2 Mixed landscapes

During the 1800s, most farms were small mixed farms that were low intensity and self-supporting: soil fertility was improved and arable weeds controlled by using rotations, fodder crops were grown for winter feed for livestock, which in turn produced organic fertiliser (Stoate 1996). However, in Britain subsidies were introduced in the 1930s with the creation of the Wheat Act, the Livestock Act and the Agricultural Development Act. These, along with the stability to farmers provided by the Agricultural Act in 1947, instigated the dramatic intensification of agriculture. By the end of the 1970s, agriculture was largely polarised: pastural farming was more common in the west and arable farming in the east (Grigg 1989; Robinson & Sutherland 2002; Figure 1.1). Even in mixed farming areas, neighbouring farms tend to specialise in the production of either crops or animals (Robinson & Sutherland 2002). This specialisation was a product of the increase in mechanisation and agro-chemical use, and the availability of resources such as fertilisers and herbicides in artificial form (Grigg 1989; Stoate 1995, 1996). This divergence of farm type was responsible for a significant decrease in landscape heterogeneity at the regional scale.

The specialisation of farms must have had significant effects on the distribution and number of hares. Although autumn densities of hares are similar in mixed and arable landscapes, numbers in pastural landscapes are low (see Chapter 2). Therefore, as farms became predominantly pastural in the west of Britain, hare numbers will have declined. Pastural landscapes, which cover a similar area of Britain to arable landscapes (pastural 28%, arable 33% area), contain just 24% of the hare population, compared to 60% in arable land (Hutchings & Harris 1996). In addition, hares are positively associated with various crops, fallow land, small areas of pasture and habitat heterogeneity (see Chapter 2), all of which are provided by mixed farmland.

6.3 Arable landscapes

6.3.1 Intensification of management and effects on hares

The area of arable land was expanded in Britain following the introduction of the Agricultural Act in 1947 (Robinson & Sutherland 2002), and management practices became increasingly intensive. Changes in separate components of management are closely interlinked, and one often facilitated another. High-yield varieties of crops were developed resulting in an increase in fertiliser use, and a move to autumn sowing. This change in timing of sowing caused the decline of winter stubbles, increased use of herbicides and further increases in fertiliser application (Stoate 1996). Nitrogen application is 50 - 80% higher on winter cereals than on spring cereals (Robinson & Sutherland 2002). The application of herbicides and fertilisers reduced the need for rotations, which had included non-cereal crops and fallow land (Robinson & Sutherland 2002). With the development of increasingly large machinery to carry out farm operations, and continued incentives to improve farming efficiency, came the removal of hedgerows to increase field size. For example, in Cambridgeshire average field size increased from 6.5ha to 16.5ha between 1945 and 1994 (Westmacott & Worthington 1997). Hedgerow density in arable counties in Britain is now only 20 - 30% of that in pastural counties, and remaining hedgerows suffered from intensive management in the 1980s, as they were regularly trimmed (Barr *et al.* 1993; Westmacott & Worthington 1997). The use of machinery also allowed synchronisation of management practices over large areas. New crops such as rape and linseed were introduced, but overall crop diversity declined. Perennial plants disappeared as farmers ploughed up to field borders and used herbicides that drifted into non-cropped areas and killed perennial plants. This allowed annual weeds to exploit the bare ground, and the growth of the most vigorous of these species was encouraged by fertiliser drift (Boatman & Wilson 1988).

The overall effect of all of these changes in management practices has been a dramatic reduction in habitat heterogeneity in terms of both species richness and structural complexity, at the field, farm and landscape scale. At the extreme, vast areas of farmland are covered by just one highly uniform crop. Set-aside land, which leads to increased habitat heterogeneity at the farm scale, was introduced as part of the Common Agricultural Policy reforms, but this measure was not rewarded by subsidy until 1992.

From this time, set-aside land was removed from production for up to five years, and its presence became much more common in the landscape (Chamberlain *et al.* 2000; Robinson & Sutherland 2002). Rotational set-aside is left to regenerate green cover over one season, and so is similar to winter stubbles; non-rotational set-aside forms a pasture-like habitat (Robinson & Sutherland 2002).

The reduction in habitat heterogeneity is likely to have caused a decline in hare numbers in arable landscapes. Hare numbers are positively associated with habitat heterogeneity throughout Europe, and although high hare numbers are associated with arable habitats, spring densities are significantly lower where arable farm management is intensive than where it is intermediate in intensity (see Chapter 2). Where farming is intensive, hares have very large home range sizes, suggesting that they increase range size to include a variety of habitats (see Chapter 3). By increasing range size, hares increase their energetic costs. This increase, unless met by an increase in food intake, causes a reduction in body condition. Hare populations are forage-limited when they are breeding in arable landscapes in spring (McLaren 1996) and in summer, particularly where crop diversity is low (Frylestam 1980a; 1986). This may explain why hares in areas of low landscape heterogeneity hares have low body condition (Frylestam 1980a), resulting in low birth rates (Frylestam 1980a; see Chapter 2). In addition, adults and leverets have low rates of survival in areas of low landscape heterogeneity (Frylestam 1980a; Hansen 1998; see Chapter 2), which suggests that recruitment rates are lower.

Low recruitment rates in intensively managed arable landscapes may be caused by poor availability of cover at particular times of year. For example, in areas of monoculture, once the crop has been harvested in the summer and the land has been ploughed, the landscape provides little cover until late winter when the new crop has emerged and gained some height. Even where a greater diversity of crops are grown, the amount of cover is fairly low over the autumn and winter due to the lack of winter stubbles and rotation crops. The last litters of leverets of the year are born during September (Raczynski 1964; Broekhuizen & Maaskamp 1981) and so without cover these will be very vulnerable to predation and adverse weather conditions. Leverets are also killed during harvesting; in an area of intensive farming in Poland, 17 hares, mainly leverets, were killed per 100 ha per year (Kaluzinski & Pielowski 1976). In addition, without cover older hares are more vulnerable to hunting by humans. Increased mortality may also have been caused by agro-chemicals sprayed in forage crops, although this is thought unlikely from the limited data available (Edwards *et al.* 2000).

6.3.2 Recommendations for management and future research

In arable landscapes, management must focus on restoring some of the habitat heterogeneity lost at all spatial scales, as well as temporally, because of the intensification of agriculture. One way to achieve this is to increase the area of non-cropped habitats such as uncultivated field margins, hedgerows, fallow land and small woodlands. These habitats provide cover and food for hares all year round and so an increase in their availability will allow rates of natality and survival to increase. Many other management practices including those pertaining to agro-chemical use, cultivation practices and rotation planning can also be targeted to increase rather than eliminate heterogeneity (Benton *et al.* 2003). For example, uncultivated field margins not sprayed with agro-chemicals have higher diversity, abundance and floristic value of vegetation than those that are sprayed (de Snoo 1999). Organic farming has strict criteria that restrict agro-chemical input and regulate the management of crops, livestock and non-crop areas such as woodlands and hedgerows (The Soil Association Certification Limited, Bristol, UK; Organic Farmers and Growers Ltd, Shrewsbury, UK). Organic farms have higher invertebrate (Wickramasinghe *et al.* in press), bird (Chamberlain, Wilson & Fuller 1999) and bat (Wickramasinghe *et al.* 2003) diversity and abundance than conventional farms, and components of habitat structure explain some of these differences (Chamberlain *et al.* 1999; Wickramasinghe *et al.* 2003). Schemes that target the re-creation of heterogeneity on conventional farms must now be developed. Farmers' attitudes and their perspectives, for example of whether uncropped land means a loss in productivity or a valuable benefit to wildlife, has a major influence on how well new management practices are taken up and therefore the effects they have on wildlife (Wilson 1996; Macdonald & Johnson 2000; Robinson & Sutherland 2002). So, if management objectives are to be successful, more attention should be given to ensuring that farmers are aware of the aims and value of management schemes in terms of biodiversity (Macdonald & Johnson 2000).

Further research on hares in arable landscapes is required to obtain additional data on demographic parameters from areas of intermediate and low intensity farming for comparison with those from areas of intensive farming (see Chapter 2). Data are required on survival rates of leverets in particular in arable landscapes, and on the causes of mortality in all age classes.

6.4 Pastural landscapes

6.4.1 Intensification of management and effects on hares

In the 1940s and 1950s, the majority of unimproved meadows in Britain were ploughed up and reseeded with high yielding grass species. This, along with the subsequent use of large amounts of nitrogen fertiliser and herbicides, has led to more productive grasslands dominated by a small number of species (Stoate 1996). Therefore, farmers can keep higher numbers of livestock on the same area of land, by lengthening the grazing period and permitting higher grazing pressure, i.e. higher livestock density. The changes also facilitated a shift from hay to silage production; silage, which provides high quality winter-feed for livestock, is cut up to four times a year starting from mid-May rather than just once, mostly in July, as hay is. Grass is also now cut at much faster rates due to improved machinery (Vickery *et al.* 2001). As in arable landscapes, to increase the efficiency of management including the use of machinery, hedgerows have been removed to enlarge field sizes.

High levels of grazing pressure by cattle reduce plant diversity (Vickery *et al.* 2001) and reduce the tussocky grass structure associated with more extensive grazing (Stoate 1996). Sheep-grazed pastures are characterised by a shorter, more homogeneous structure than cattle grazed pastures (Fuller & Gough 1999; Vickery *et al.* 1999; Benton *et al.* 2003), and while numbers of cattle have decreased, numbers of sheep have increased significantly since the 1970s (Fuller & Gough 1999; Chamberlain *et al.* 2000; see section *2.4.4*). These changes, along with grazing management based on grass heights and buffer feeding strategies (offering hay, silage or straw mixtures in times of grass shortage), which are adopted to sustain maximum utilisation of pasture and animal production (Frame, Baker & Henderson 1995) mean that intensively managed grassland is structurally uniform throughout the year.

Hare numbers are lower in pastural landscapes than in arable landscapes throughout Europe, suggesting that the two habitats have always supported different numbers of hares. In Britain, the density of hares in pastural landscape is approximately half that in arable landscapes (Hutchings & Harris 1996). However, in the 1960s hares were described as common in both arable and pastural landscapes (Corbet 1966)

suggesting that numbers have declined at a faster rate in pastural landscapes than in arable landscapes.

The intensification of grassland management has resulted in increasing levels of disturbance to hares due to increased livestock densities, the presence of livestock for a greater proportion of the year, and increases in chemical applications and grass cutting. Hares are thought to avoid pasture grazed by cattle because of the disturbance caused to their normal activities (Frylestam 1976; Barnes *et al.* 1983). However, in common with Vaughan *et al.* (2003), I found no evidence for avoidance of cattle at densities up to 8.2 LSU ha^{-1}; instead hares tend to select pastures grazed by cattle throughout the year (see Chapter 3). Silage cutting increases leveret mortality and therefore decreases recruitment: 46% of leverets in silage fields compared to 17% of those in hay meadows are killed by machinery (Kaluzinski & Pielowski 1976).

Disturbance may contribute to the low abundance of hares in pastural landscapes. However, as in arable landscapes, the most significant change in pastural habitats has been the loss of heterogeneity in terms of species diversity and structure at field, farm and landscape scales. Hares are associated with habitat heterogeneity (see Chapter 2), and require heterogeneous habitat structures throughout the year in pastural landscapes (see Chapter 3). Heterogeneity at the between-habitat (farm) scale does not appear to be very important to hares, but is likely to be more important where management is more intensive. The loss of heterogeneity within and between grass fields is likely to have had significant effects on hare numbers. High hare numbers are strongly associated with unimproved grassland (Hutchings & Harris 1996), a habitat that has largely been removed from the landscape.

Hares in pastural landscapes are less likely to participate in breeding (Appendix 2), have lower rates of fecundity and lower juvenile survival than those in arable landscapes; adult survival is similar in hares in the two landscapes (see Chapter 5). Lower rates of fecundity are likely to be due to poor body condition (Frylestam 1980a; Appendix 2). This may be due to low forage quality during the autumn (see Chapter 4), but is more likely to be due to poor quality habitat in terms of cover (see Chapter 3). Hares are positively associated with cover (see Chapter 2), and without good quality cover, hares are susceptible to predation and exposure. Increased energy demands result from higher levels of predator evasion activity and higher rates of thermoregulation reducing body condition. Hares of lower body condition not only have lower rates of fecundity, but are also more vulnerable to mortality due to disease

and predation. Hares select taller habitat structures during the breeding season (see Chapter 3), and poor quality cover is likely to increase mortality rates in leverets in particular. Therefore, hare populations are limited by recruitment in pastural landscapes because low habitat heterogeneity leads to available cover being of poor quality.

6.4.2 Recommendations for management and future research

Hares in pastural landscapes are associated with arable land (Hutchings & Harris 1996). However, results of my study did not suggest that populations are limited by the availability of arable land within a pastural landscape. In intensively managed grasslands the conversion of some fields to arable crops would increase habitat heterogeneity, and so would increase the availability of cover at certain times of year, which would benefit hares. However, the conversion of grassland to arable crops within pastural landscapes is unlikely to have significant effects on hare numbers.

In pastural landscapes there needs to be a move away from the management of grassland for maximum productivity, which leads to structural uniformity between and within fields throughout the year (Frame *et al.* 1995). Support should be given to farmers to make the restoration of lower-input, more extensive livestock systems more feasible. Support payments should be based on area rather than the amount of production (Vickery *et al.* 2001). More extensive systems would increase habitat heterogeneity at the within- and between-field scales. For example, seasonal rather than continuous grazing is likely to promote heterogeneous vegetation structure (Morris 1973). A reduction in livestock densities would also allow a reduction in intensity of silage production; fewer cuts per year would mean a decrease in leveret mortality. Restrictions on cutting in spring would have the greatest effect on leveret mortality, as natalities are highest between April and June (Lincoln 1974; Hewson & Taylor 1975; Boekhuizen & Maaskamp 1981). Farmers should be encouraged to have some woodland, fallow land and ungrazed fields, in order to increase heterogeneity at the within- and between-habitat scales. They should also be encouraged to leave uncultivated field margins to increase within-field heterogeneity. The management of these margins for biodiversity is an accepted practice in arable systems (Vickery *et al.* 2001). A programme of habitat change that increased permanent cover and

heterogeneity showed that increased numbers of hares result from improving habitat quality (Slamečka 1991). If hares are provided with habitat heterogeneity, particularly in terms of structure at the within-field level, they will achieve higher rates of recruitment and therefore higher population numbers in pastural landscapes.

Further research on hares in pastural landscapes is required to obtain data on demographic parameters and abundance in areas managed at different levels of intensity. Data are also needed on habitat selection, fecundity rates, survival rates and causes of mortality in areas with varying levels of habitat heterogeneity to see how factors such as vegetation structure affect these. In particular, additional information on the survival of leverets in pastural landscapes is required.

6.5 Is an increase in hare population numbers feasible?

In Chapter 5 I showed that hare populations in arable landscapes in Britain could be doubled within the next ten years. However, hares are already common in these areas, meaning that populations in pastural landscapes need to be targeted if the BAP target is to be reached (McLaren *et al.* 1997). To achieve similar increases in populations in pastural landscapes requires increases in parameters to values higher than those recorded in real populations (see Chapter 5). Even if a doubling of populations were possible in pastural landscapes, this would still not be enough to double the hare population in Britain, as starting population numbers in these areas are lower than in arable landscapes (Hutchings & Harris 1996; see Chapter 2).

Although achievement of the UK BAP objective to double spring numbers by 2010 (Anonymous 1995) is not feasible, maintaining and expanding existing populations are more realistic goals. Results from projection modelling and a questionnaire study suggest that hare populations in arable landscapes are already expanding, or are stable (Vaughan *et al.* 2003; see Chapter 5). This is likely to be due to agricultural management policies developed over the last decade which address some of the effects of intensification, including the introduction of subsidies for set-aside and the schemes discussed below. Management must now focus on pastural landscapes in an attempt to stabilise declining hare populations in these areas (see Chapter 5). Data collected for the British Trust for Ornithology's Breeding Bird Survey between 1995

and 2000 suggest that hare abundance has declined throughout Britain, and has declined significantly in the pastural southwest of Britain (Newson & Noble 2002).

In European Union countries there are a number of schemes designed to improve agricultural landscapes for wildlife including the Special Area of Conservation and the Less Favoured Area schemes. Governments have also encouraged initiatives at the national, regional and local level, such as Environmentally Sensitive Areas, and the Countryside Stewardship Scheme in England that is largely focussed on pastural areas (Ovenden, Swash & Smallshire 1998). These schemes can be used as the basis for encouraging changes in grassland management such as those discussed in section *6.4.2*. For example, in Environmentally Sensitive Areas in the Yorkshire Dales, farmers are paid to manage species-rich hay meadows by using traditional methods with restrictions on fertiliser applications and dates of cutting (Green 1990). As part of the 1992 Common Agricultural Policy reforms, provisions for financial support were included for traditional farming farming systems and extensification options (Vickery *et al.* 2001). Although at present such environmental schemes do not specifically target the creation and management of habitat heterogeneity on farmland, this should now be an objective included within agri-environment policies. From a management perspective, enhancing habitat heterogeneity is easiest, both logistically and politically, at the field and farm scale (Benton *et al.* 2003). However, if the distribution of changes in management is widespread, they will result in landscapes with habitat heterogeneity throughout the year, and so lead to heterogeneity at field, farm and landscape scales.

Targeting management for habitat heterogeneity at these different scales ensures that a wide variety of farmland species benefit. It also helps to alleviate the problem of favouring management for certain taxa at the expense of others, as habitat heterogeneity provides resources for species-rich communities of organisms (Benton *et al.* 2003). The species approach not only creates problems of priorities, but is also problematic as individual species have complex interactions with farm management practices throughout the year that are rarely understood. This means that at present, and without further research, it is difficult to put in place specific conditions to ensure the survival of many of the declining farmland species (McCracken & Bignal 1998). By using a more general approach, which attempts to re-establish some of the features of agricultural habitats that have been lost over the last few decades, it is more likely that biodiversity as a whole will benefit.

Habitat loss is an important driver of population declines and biodiversity loss. However, in European agricultural landscapes, more intensive management, degradation in habitat quality and increasing habitat homogeneity are most responsible for the decline in biodiversity (Robinson & Sutherland 2002). Therefore, it is crucial that we address some of the habitat changes resulting from agricultural intensification, and in particular regenerate some of the heterogeneity lost at all scales. This will not only benefit hare numbers, by creating better quality food and cover throughout the year resulting in higher fecundity and survival rates, but will benefit farmland biodiversity as a whole. With changes in habitat management, and with further research and monitoring, farmland species such as the European hare will once more become a common sight throughout the British countryside.

6.6 Approaches to the study of population regulation

An understanding of population regulation is fundamental to population ecology, including all areas of wildlife management (see Chapter 1). The objective of management may be to increase, maintain or decrease population growth rate in a given species, for the purpose of conservation, sustainable harvesting or reducing pest species. Without knowledge of the impact of different factors on population numbers, effective management is not achievable.

A wide range of factors affect population growth rate, and so a number of approaches can be used to study population regulation. Factors fall into two main categories: researchers can either focus on the effects of regulatory factors such as climate, predation, food resources or competition on population numbers (e.g. Keith *et al.* 1977; Newsome, Parer & Catling 1989), or they can investigate the relationship between demographic parameters and population growth rates (e.g. Cuthbert, Fletcher & Davis 2001; Lalas & Bradshaw 2003). The majority of researchers concentrate on one of these approaches, or they investigate a specific combination such as how fecundity and/or survival are affected by habitat availability (e.g. Moreno, Villafuerte, Delibes 1996; Pye *et al.* 1999) or climate (Nager & Noordwijk 1992; Milner *et al.* 1999; Redpath *et al.* 2002). A number of different methodologies are also available to ecologists for these studies, including the analysis of observational (e.g. Keith *et al.*

1977) or experimental data (e.g. Pech *et al.* 1992; Byrom *et al.* 2000), or population modelling (e.g. Brault & Caswell 1993; McCarthy 1996). Turchin (1999) suggested that the narrow focus on manipulation experiments used by many researchers, particularly those in North America, to answer ecological questions should be replaced by studies synthesising all three methodologies. He believes that experimental techniques are most powerful at the later stages of studies into population dynamics, following methods such as time-series analysis, which helps to reduce the number of viable hypotheses, and mathematical modelling of potential limiting factors, to obtain predictions that can then be tested experimentally.

In this study, I have not just taken one of the possible approaches to investigate population regulation of the hare, nor have I concentrated on examining the effect of one regulatory factor on one aspect of demography. Instead I have used a more holistic approach. I have investigated the effects of regulatory factors such as climate, habitat availability and predators on both population numbers and demographics, using long-term data sets and data collected in the field. I have also examined how demographic parameters affect population growth rates using projection models. By using a holistic approach, rather than studying one very specific question, I have been able to get a better understanding of how both regulatory factors and demographic factors affect hare population numbers, and how they interact to limit populations (Table 6.1). Only by taking this approach have I been able to determine which factors have led to the decline of the European hare, and how management to achieve population growth should be targeted. I have identified which resources should be managed to produce increases in the demographic parameters that limit population numbers, and so will result in the largest increase in population numbers. By using projection models I have also determined the magnitude of parameter increases required to produce population growth in declining populations, and whether desired population increases are feasible. The next step would be to carry out habitat manipulation experiments to determine how hare populations respond to changes in the resources identified as limiting hare numbers.

My work has demonstrated the value of the holistic approach to the study of population regulation and wildlife management. It is of course important to continue investigating specific questions of regulation for different species, to get a more in depth understanding of how particular factors affect population numbers, and how certain factors interact. However, such studies are only valuable as one piece of a puzzle, which must be fitted together to get a full understanding of what regulates a

particular population. Management schemes that are developed without a full understanding of which factors affect population numbers of the target species can waste valuable time and resources; schemes may either have no impact on numbers, or they may adversely affect the target population or other species.

Table 6.1 Key factors that may have caused population decline and limit population numbers of hares in pastural and arable landscapes; factors not investigated in this study are indicated.

Factor	Caused decline or limits populations	
	Pastural landscape	**Arable landscape**
Regulatory factors		
Climate	} Depends on cover	} Depends on cover
Predation		
Hunting by man	No	?
Disease	*Not studied*	*Not studied*
Resources - Food	No	} Yes; not investigated separately
- Cover	Yes	
- Space	No	No
Demographic factors		
Natality	Yes	Likely
Mortality - Adults	No	?
- Juveniles	Yes	Likely
Immigration	*Not studied*	*Not studied*
Emigration	*Not studied*	*Not studied*

A better understanding of population regulation is vital not only for successful management of ecosystems on a regional scale, but also for understanding the global changes that now face our planet. This can be achieved most effectively by using a comprehensive approach to the study of population regulation, taking into account the effects of a wide range of factors on population growth rates and using several methodologies. This approach will be of benefit to ecologists and wildlife managers alike, in many different fields of biology.

Chapter 7

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Appendices

Appendix 1

Density estimates at the study site from spotlight counts (Buckland *et al.* 1993; Distance 4.1 Release 2), with the model used and cut points (Péroux *et al.* 1998); CV = confidence value, CI = confidence intervals.

Year	Month	Model	Cut points (m)		Density (hares 100 ha^{-1}) Estimate	CV (%)	95% CI	
2000	October	Uniform + simple polynomial	160	300	17.60	21.49	11.35	27.30
2001	October	Half-normal	180	350	15.34	23.27	9.64	24.42
2002	March	Uniform + simple polynomial	180	420	12.99	16.49	9.27	18.20
2002	October	Uniform + cosine	180	300	14.88	25.43	9.00	24.61
2003	March	Half-normal	140	320	13.05	22.28	8.40	20.27

Appendix 2

Jennings, N.V., Smith, R.K., Hackländer, K., Harris, S. & White, P.C.L. Variation in demography, condition, and dietary quality of hares *Lepus europaeus* from high-density and low-density populations. *Wildlife Biology*, submitted.

Variation in demography, condition, and dietary quality of hares *Lepus europaeus* from high-density and low-density populations

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Abstract

Numbers of European hares *Lepus europaeus* have declined throughout Europe due to agricultural intensification. However, hares are more common in areas used for intensive arable crop production than in pastural areas. To identify factors which may limit populations of this species, functional explanations for current differences in the density of hares were sought. The demography (litter size, prenatal mortality and participation in breeding by females), body condition (urinary and serum nitrogen, kidney fat, bone marrow fat, skeletal size and body weight), and dietary quality (ash, protein, fat, fibre, carbohydrates, and total weight and energy in stomach contents) of hares from parts of England and Wales where they are currently present at relatively high densities (arable habitats) and at relatively low densities (pastural habitats) were compared. Regardless of the definition of habitats (by land classification system or annual census of farmers), in pastural areas a lower proportion of adult females were lactating in late winter than in arable areas. Recruitment was therefore lower in pastural than in arable habitats. Hares from pastural areas were smaller, lighter, and had less fat than those from arable areas, but dietary quality was similar. Thus hares in low-density populations from pastural areas were able to obtain a good-quality diet, but expended more energy and were unable to maintain body condition as well as those from arable areas. Pastural habitat, which in England and Wales is relatively warm and wet, is sub-optimal for hares. The reduced recruitment and chance of survival of hares in pastural habitats we describe may help to explain the observed differences in density of hares in arable and pastural habitats. Efforts to conserve the hare should focus on the reduction of predation and exposure to unfavourable weather by the provision of year-round

vegetative cover (such as fallow land, rough grassland, and shelterbelts), to increase the chances of survival of leverets and adult hares.

Introduction

The European hare *Lepus europaeus* is protected under Appendix III of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; Anonymous 1979). It is classed as a 'priority species of conservation concern' by the UK government, and therefore has a Biodiversity Action Plan (BAP), the aim of which is to increase numbers of hares (Anonymous 1995). Records of hares shot each year suggest that numbers have declined in recent decades throughout Europe (Pielowski & Pucek 1976, Tapper 1992), and agricultural intensification has been blamed for the decline (Tapper & Barnes 1986, Slamečka 1991). Populations of hares may decline if agriculture becomes very intensive (Tapper & Barnes 1986, Slamečka 1991, Panek & Kamieniarz 1999). However, throughout Europe, the hare is more common in intensively farmed arable areas than in pasture and other non-arable areas (Hutchings & Harris 1996, Klansek et al. 1998, Vaughan et al. 2003, Smith et al. in press a).

It is unclear what limits populations of hares, although nutrition (Frylestam 1980a, Hackländer, Tataruch & Ruf 2002), predation (Lindström et al. 1994), and climate or exposure to unfavourable weather conditions (Hackländer, Arnold & Ruf 2002) have been suggested, and may affect recruitment and survival. A high-fat diet increases female reproductive rate (Hackländer, Tataruch & Ruf 2002). Hares in mainly pastural areas of low habitat diversity have higher mortality rates and lower body weights than those in diverse mixed arable landscapes (Frylestam 1980a). Increased numbers of hares have resulted both from improving habitat quality without

manipulation of predator numbers (Slamečka 1991; for snowshoe hares *Lepus americanus* O'Donoghue & Krebs 1992), and from removal of foxes *Vulpes vulpes* (the main predator of the hare) without any change in habitat (Lindström et al. 1994). Weather conditions are correlated with numbers of hares (precipitation negatively and temperature positively; Nyenhuis 1995).

In this paper, we seek functional explanations of variations in abundance of hares through measurement of selected demographic and other parameters, as advocated by Marboutin & Péroux (1995) and Vaughan et al. (2003). We quantify pre-breeding population age structure, litter size, incidence of prenatal mortality, and for females, percentage of young and adult hares breeding. We also quantify potential covariates of demographic parameters: body condition, skeletal size, and body weight (Frylestam 1980a, Marboutin et al. 1990), and describe dietary quality (ash, protein, fat, fibre, carbohydrates, and total energy). We compare these parameters for hares from relatively high-density populations in cool and dry arable areas (mainly in the east of England; mean January temperature 3-4°C, mean annual precipitation 466-740mm) with those for hares from relatively low-density populations in warm and wet pastural areas (mainly in the west; mean January temperature 4-8°C, mean annual precipitation 741-4577mm; averages for 1971-2000, UK Meteorological Office; www.met-office.gov.uk). We also quantify the weather conditions experienced by hares in the locations and years in which we sampled them.

We test the hypothesis that pastural habitats support relatively low densities of hares because they are sub-optimal in terms of nutrition. Therefore, we expect hares from pastural areas to have poor quality diets, poor body condition, and to perform badly in terms of reproduction compared with hares from arable areas. If nutrition is important in limiting the growth of populations of hares in pastural areas, habitat management could benefit populations and help conservation targets to be reached. We

evaluate the likely effectiveness of farmland habitat management for increasing numbers of hares in line with the BAP objectives.

Material and methods

Study animals

We obtained 1010 hare carcasses, but discarded 86 because we were unable to determine their age or gender, or they were not judged healthy at necropsy (n=27, no association was found between habitat of origin and disease). We were left with a sample of 920 carcasses from 125 locations in England and Wales (Fig. 1). Carcasses were collected in 1998-2001 (all habitats were sampled in each of these years); 774 were from 26 shooting estates in England, the remaining 146 were mainly killed by cars and collected by volunteers. We processed carcasses within a few hours of death in the field when possible, or brought them fresh or frozen to the laboratory for processing, within 24 hours of death if fresh.

Age determination

We used three methods for age determination. We estimated the ages in days of animals ≤454 days old from the arithmetic mean of the two eye lens weights (Suchentrunk, Willing & Hartl 1991). The mean weights were repeatable (r_I = 0.999, $F_{19,40}$=3602, P <0.0001; Zar 1999).

The mandibles of hares for which no eye lenses were available, and of those which were estimated from the eye lens weight to be >454 days old, were cleaned and dried for 48 hours at 60°C in an oven (Hearson). We sent them to Matson's Laboratory LLC (PO Box 308, 8140 Flagler Road, Milltown MT, USA) for sectioning and age

analysis (to the nearest year) from adhesion lines in periosteal tissue (Frylestam & von Schantz 1977).

We used the presence of an epiphyseal protusion at the lateral ulnar knob ('Stroh's sign'; Stroh 1931) to indicate animals aged ≤234 days (7.7 months). At this age, 50% of hares also aged by eye lens weights had lost their protusion (Suchentrunk et al. 1991).

Of the 920 hares, the ages of 892 (97%) were determined using at least one of the most robust methods (eye lens weights or adhesion lines in mandibles). When more than one method was used, results were consistent.

The youngest hare in our sample was three months old and therefore independent (weaning occurs at *c.* 30 days, range 23->67 days; Broekhuizen & Maaskamp 1980). Hares were defined as 'adult' if older than 7.7 months (≥234 days, i.e. sexually mature; Raczyński 1964, Broekhuizen & Maaskamp 1981, and fully grown; Stroh 1931) and as 'young' if aged <7.7 months. Depending on their time of year of birth, hares may breed as young as four months, but all hares aged *c.* eight months can breed (Broekhuizen & Maaskamp 1981).

Reproduction in females

We noted signs of lactation. Since milk is present in the mammary glands of rabbits *Oryctolagus cuniculus* in the last few days of pregnancy (Brambell 1942), we did not class female hares as lactating if their embryos were near full-term (age of embryo ≥38 days since conception based on weight; Broekhuizen & Martinet 1979). This was the case for 21 females. Females were classed as pregnant if embryos were visible by eye. In rabbits, blastocysts are undetectable macroscopically for the first three days (10%) of the gestation period (Brambell 1942). If early pregnancy in hares is similar, we missed

all pre-implantation pregnancies in the first 4.3 days (approximately 10% of pregnancies; the gestation period in the hare is *c.* 43 days; Martinet, Legouis & Moret 1970, Stavy & Terkel 1992).

The uteri of non-pregnant females were cut longitudinally along each horn and examined for recent uterine scars (Hansen 1992, Bray et al. 2003). We used scars classed as <48 days old, found only in lactating females, to determine the number of leverets in the litter currently sucking (Bray et al. 2003). From these scars, we calculated the six-week period of birth (season; defined as: early spring = 22 March - 6 May, late spring = 7 May - 21 June, early summer = 22 June - 7 August, late summer = 8 August - 23 September, early autumn = 24 September - 7 November, late autumn = 8 November - 21 December, early winter = 22 December - 3 February, and late winter = 4 February - 21 March) for sucking litters by assuming they had been born 15 days before (i.e. were half-way through the suckling period of *c.* 30 days).

The uteri of pregnant females were stored in 10% formaldehyde solution until re-examination, when numbers of viable and resorbing embryos were counted (Raczyński 1964). We were thus able to quantify post-implantation resorption. We could not quantify pre-implantation resorption. We may have missed very early resorption if the female was not killed until much later in the pregnancy, and any resorption which may have occurred had the female not been killed. We removed embryos (n=311) from the uterus and aged them to the day of gestation (Broekhuizen & Martinet 1979) so that we could predict the season of birth.

Seasons of birth of litters were predicted from pregnancies and from uterine scars, but not from both for the same female. In females which were pregnant and lactating, we calculated the season of birth from pregnancy since this was more accurate. Females carrying resorbing embryos could be pregnant (with a litter including both resorbing and viable embryos), but were classed as non-pregnant if carrying only

resorbing embryos. We quantified prenatal mortality as the percentage of all embryos resorbing (Raczyński 1964) and as the percentage of litters which included only resorbing, and resorbing and viable embryos.

Body condition

We used several methods to quantify body condition in adult hares (Henke & Demarais 1990).

The urinary urea nitrogen (mg/dl) to creatinine (mg/dl) ratio (UN:C) and the serum urea nitrogen concentration both provide a snapshot view of the quality of an animal's diet. We quantified UN:C in urine samples. More urea nitrogen is found in urine as protein intake increases. It is standardised with respect to creatinine, because while urine concentration varies, creatinine is excreted at a constant rate (Delgiudice, Mech & Seal 1990, Villafuerte, Litvaitis, & Smith 1997). We measured levels of urea and creatinine spectrophotometrically in diluted urine samples (1:20 with saline solution) by using reagent kits and an autoanalyser (Konelab 30i; Konelab Corporation, Ruukintie, Finland). As urine was not available from all hares, we took blood samples (*c.* 5ml) from the thoracic cavity within three hours of death and centrifuged them (Searle: B400 centrifuge). We measured levels of serum urea (mMol/l) spectrophotometrically using reagent kits and an autoanalyser (Konelab 30i; Konelab Corporation, Ruukintie, Finland), and converted them to serum nitrogen (mg/dl; SUN).

The kidney fat score reflects the nutritional status of the hare in the medium term (<*c.* 2 weeks; Henke & Demarais 1990). N.V.J. estimated fat levels around kidneys and on either side of the body cavity (total perirenal fat; Monson et al. 1974) on a scale of 0-8. A kidney fat score of 0 indicated that no fat was visible, and a score of 8 indicated that the areas examined were completely filled with fat.

The bone marrow fat index provides a long-term indication of body condition, as bone marrow fat is mobilised after kidney fat (Riney 1955, Henke & Demarais 1990). Bone marrow fat is mobilised after several weeks on a restricted diet (in cottontail rabbits *Sylvilagus floridanus;* Warren & Kirkpatrick 1978). We removed marrow (0.5-1.5g wet weight) from each femur. Marrow was weighed (Oertling: R20 balance, accuracy 0.0001g), dried to constant weight for 72 hours at 70°C in an oven (Hearson), then reweighed. We calculated the bone marrow fat index as the mass of the dried marrow as a percentage of its original fresh weight (Keith et al. 1984).

The skeletal size and cleaned weight provide long-term indicators of body condition; body size reflects food availability during the period of skeletal growth (i.e. the first *c.* 8 months of life). To quantify skeletal size, N.V.J. measured the length of the hind foot with a modified ruler (accuracy 0.1cm). Lengths were repeatable (hind foot r_I=0.948, $F_{9,20}$=55.7, P<0.0001). We took body weights and cleaned weights (weight after removal of liver, reproductive tract and digestive tract from below the diaphragm; Salter: 235 6S scale, accuracy 10g).

Dietary quality

We weighed stomachs full and empty of contents. Contents were mixed, oven-dried (72 hours at 60°C), milled to 1mm fragments (Culatti mill), mixed again, and analysed for % dry matter, % ash, % crude protein, % crude fat, % crude fibre, and % carbohydrate content. We calculated the dry weight of the stomach contents from the % dry matter and the total wet weight. Energy content of stomach contents was calculated using Atwater factors; the digestible energy of fat, protein, and carbohydrates were assumed to be 37.7, 16.7 and 16.7 kJ g^{-1}, respectively (see Hackländer, Tataruch & Ruf 2002).

Allocation of hares to arable or pastural habitats, and climatic data

The location of origin for each hare was represented by an Ordnance Survey grid reference. For the 2500ha square which contained each grid reference, we obtained mean annual precipitation (mm) and mean January temperature (°C) for the years 1997-2000 from the UK Meteorological Office (www.met-office.gov.uk). We included data for 1997 since many of our hares were killed in February 1998, and could not include data from 2001 since they were not available. We obtained data on the habitat in the location of each grid reference from the land class database (held by the Centre for Ecology and Hydrology (CEH); Bunce *et al.* 1996), and from the annual agricultural census database for 1999 ('June census') held by the UK government's Department for Environment, Food and Rural Affairs (DEFRA) and the Geographical Information (GI) Services Branch of the National Assembly for Wales. Allocation to a land class is based on geology and soil type. The June census data reflect crops actually grown on farmland and can therefore be altered through land management, although the distribution of arable and pastural land changes little from year to year.

Data from the land class database

We allocated the 100ha square represented by each grid reference to levels of CEH's land classification system ('landscape types': arable a, arable b, arable c, pastural, and marginal upland; Bunce et al. 1996; see Table 1). Less than 5% of hares were from arable c and marginal upland landscape types. Densities of hares in the remaining landscape types, surveyed 1991-1993, were: arable a: 3.3 hares 100ha $^{-1}$, arable b: 9.0 hares 100ha $^{-1}$, pastural: 3.0 hares 100ha $^{-1}$ (Hutchings & Harris 1996). Arable a and b landscape types are similar in land use and geology, but arable a occurs in southern England and arable b in eastern and central England. The pastural landscape type occurs mainly in the west of England and in Wales (Bunce et al. 1996).

Data from the June census

Our June census data were pooled for parish groups. In England there were 1263 parish groups, which had a mean area of 10,526 ha of agricultural land (range 0.9-77,804 ha). In Wales, the 'small area', of which there were 235, is comparable. 'Parish group' is used here to refer to both. The 'farmland type' in the parish group of origin of each hare was derived from the total area of land in agricultural use and areas used for crops and setaside, and pasture (Table 1). If >50% of the area of a parish group was a certain farmland type, it was allocated to that type. Hares are much more common in arable farmland types than in pastural farmland types (Vaughan et al. 2003).

Paired sampling

For some analyses, particularly when sample sizes were small, a precise and powerful comparison between hares from areas which support high and low densities of hares was desirable. Therefore, and since the arable b landscape type supports high densities of hares while pastural and marginal upland landscape types support similar and much lower densities of hares, hares from arable b were chosen at random from all suitable hares to form matched pairs with hares from the pastural (64 pairs) and marginal upland landscape types (16 pairs). Marginal upland supports *c.* 2.50 hares 100ha $^{-1}$ (Hutchings & Harris 1996), and is mostly pasture (Bunce et al. 1996). Pairs (78 in total; 41 adult male pairs and 37 adult female pairs) were matched with regard to gender, time of year of death, and cause of death. The time of day of death was not always known, but was matched as far as possible, since the cause of death was matched within pairs. The mean number of days between the deaths of members of the pairs was 10 (range 0-29).

Statistical analysis

We carried out analysis on SPSS 10 (Field 2000), with a significance level (α) of 0.05 unless stated otherwise, and examined carcasses and samples blind. We compared parameters between hares allocated to landscape types and farmland types (Table 1). In χ^2 analysis, levels were omitted if their inclusion resulted in an average expected frequency of <6 (Zar 1999).

For the body condition, size and weight variables, we developed a separate logistic regression model for each gender. Collinearity existed between body weight and cleaned weight, so we excluded body weight from the analysis. We carried out simple analyses with the dependent variables landscape type and farmland type, to select variables for inclusion in the final models. We subtracted the deviance (-2 log likelihood) of the null model from that of each simple model, and tested the difference (Δd) for significance (χ^2 distribution; log-likelihood test). We included variables with significant log-likelihood tests in final models (α=0.1; Hosmer & Lemeshow 2000). The significance of each final model was tested by the log-likelihood test, and overall fit was quantified by the deviance goodness-of-fit test (Hosmer & Lemeshow 2000).

We analysed paired samples by means of repeated-measures analyses of variance (ANOVAs), in which habitat was a within-pair factor and gender was a between-pair factor. We checked for sphericity (Mauchly's test) and for homogeneity of variances (Levene's test; Field 2000) and transformed variables if necessary to conform to the assumptions of ANOVA.

Since hares are rarely shot except in February in England and Wales, sample sizes from other times of year were often too small for comparison. Also, not all parameters could be measured from each carcass, so sample sizes varied between

analyses. Statistical analysis is limited to seasons and age classes of hares for which the sample size was considered large enough.

Results

Of the 920 hares, 418 were adult males, 390 were adult females, 61 were young males, and 51 were young females; 67 were killed in spring, 35 in summer, 47 in autumn, and 768 in winter. Of the 156 paired hares, 32 were killed in spring, 10 in summer, 18 in autumn, and 96 in winter.

Demography

Population age structure, litter size and prenatal mortality

Of males and females killed in winter (pre-breeding), *c.* 30% were <1 year old (males: 32%, total *n*= 397; females: 29%, total *n*=361). 6% of males, and 15% of females were >3 years old. We found no effect of landscape or farmland type on pre-breeding age structure.

Litter size (number of recent scars or embryos) was examined in adult females which were predicted to give birth or have given birth in late winter and early spring. The median size of litters was 1 (range 1-4; *n*=151) in late winter, and 2 (range 1-5, *n*=54) in early spring. Kruskal-Wallis and Mann-Whitney tests were used to compare litter sizes between the landscape and farmland types; no significant differences were found in late winter or in early spring.

In females killed in late winter, of 318 embryos examined, 14% were resorbing. Of the 206 litters examined, 11% contained at least one viable and one resorbing embryo, and 6% contained only one or more resorbing embryos. These figures were

highly consistent across landscape and farmland types. We found no resorption at other times of year (41 embryos in 19 litters examined).

Percentage of young females breeding

Of 35 young females killed in winter, 60% were pregnant and 9% were lactating. In winter, more young females than expected were breeding in the arable farmland type, and fewer than expected were breeding in the pastural farmland type (χ^2=5.358, df=1, *P*=0.020; Table 2). No significant difference in participation in breeding by young females due to landscape type was found.

Percentage of adult females breeding

Of adult females in spring, 50% were pregnant (total *n*=22) and 71 % (*n*=17) were lactating; in summer, 19% were pregnant (*n*=16) and 47% were lactating (*n*=15); in autumn, 10% were pregnant (*n*=10) and 11% were lactating (*n*=9); in winter, 61% were pregnant (*n*=331) and 32% were lactating (*n*=225). Since there was a large increase in participation in breeding throughout the winter (17% pregnant in early winter and 64% pregnant in late winter), we compared numbers of adult females pregnant and lactating in late winter in landscape and farmland types (Table 3); we found no significant differences in incidence of pregnancy. Incidence of lactation was higher than expected in arable a and lower than expected in arable b and pastural landscape types (χ^2=22.265, df=2, *P*=0.000). Adult females from pastural farmland types were also less likely to be lactating than those from arable farmland types (χ^2=8.368, df=1, *P*=0.004).

Body condition

We collected data on body condition for adult hares (Table 4). We derived logistic regression models to compare hares killed in winter in various landscape and farmland types. Both male and female hares from arable landscape types were significantly larger and heavier than those from pastural landscape types. Differences between hares from different farmland types were less clear. Overall, the directionality of responses was highly consistent. Hares from areas where hare density is high (*i.e.* arable areas) were heavier than hares from areas of low density (Table 5).

We also compared body condition in 78 matched pairs of hares (Table 6). Analyses revealed effects of habitat on kidney fat score, hind foot length and cleaned weight. Hares from arable areas are fatter (median fat score = 3 for arable and 2 for pastural hares), bigger (mean hind foot length = 14.3cm for arable and 14.1cm for pastural hares), and heavier (mean cleaned weight = 2.7kg for arable and 2.5kg for pastural hares) than hares from pastural areas. There were no effects of gender or of the gender x habitat interaction (Table 6).

Dietary quality

Our analysis of dietary quality for 40 matched pairs of hares (18 male pairs and 22 female pairs; Table 7) revealed significant effects of habitat on % ash (higher in arable hares than in pastural hares), % fibre (lower in arable hares than pastural hares), and % carbohydrates (lower in arable hares than in pastural hares). Effects of gender occurred in % protein (higher in males than in females) and % fibre (lower in males than in females; Table 8). Therefore dietary quality, amount of dry matter consumed, and amount of energy consumed is similar in both habitats. There is no evidence to suggest that hares in arable areas are able to obtain a better quality diet than hares in pastural areas.

Climate

We found a significant difference in mean annual precipitation due to landscape type; mean annual precipitation was significantly lower in arable b (734mm) than in arable a (899mm) and in pastural landscape types (1011mm; oneway ANOVA; F_2=30.74, *P*=0.000). A significant difference was also found due to farmland type; mean annual precipitation was lower in the arable farmland type (736mm) than in the pastural landscape type (1173mm; oneway ANOVA, F_1=86.24, *P*=0.000;). In the years in which sampling for hares took place, in the locations from which our hares originated, wetter conditions were experienced in pastural landscape types and farmland types than in arable areas.

We found a significant difference in mean January temperature due to landscape type; mean January temperature was similar in arable a (4.1°C) and arable b (4.2°C), and significantly higher in the pastural landscape type (4.7°C; oneway ANOVA; F_2=13.12, *P*=0.000). Hares from pastural landscape types experienced higher January temperatures than those from arable landscape types. Mean January temperature in arable (4.1°C) and pastural farmland types (4.4°C) was similar (oneway ANOVA; F_1=3.21, *P*=0.076).

Discussion

Demography

Population age structure, litter size, and prenatal mortality

In common with Pielowski (1971), we found older females than males in the population. Litter sizes given here for late winter and early spring are not directly comparable with those in the literature, since we used the predicted season of birth.

Litter size is unrelated to habitat, and to nutrition (O'Donoghue & Krebs 1992, Hackländer, Tataruch & Ruf 2002), but it is related to weather conditions (Hewson & Taylor 1975).

We found typical rates of prenatal mortality for late winter (14% of embryos): in the east of England, 14% of litters were resorbed (Lloyd 1968), in the Russian Federation, 24% of females pregnant in January had resorbing embryos (Kolosov 1941). In Poland in February-April 6-10% of embryos, but in January 80% of embryos were resorbed (Raczyński 1964).

Percentage of females breeding

The percentage of young females we found breeding in winter differed between farmland types. In the east of England 4% (Lincoln 1974), and in France about 14% (Bray 1998) of females breed in their year of birth. Lloyd (1968) found 37% of young females killed in winter in the east of England to be pregnant; we found 60%.

Although we found no effect of landscape type or farmland type on percentage of adult females pregnant, the incidence of pregnancy we found in late winter, spring and summer was low compared to that found by others using similar methods to define pregnancy (60-100% in Scotland, Hewson 1964; *c.* 80% in the Netherlands, Broekhuizen & Maaskamp 1981). Pregnancy rate in arable areas in Poland differed between consecutive Februaries (44 and 85%; Raczyński 1964), and is probably variable, particularly at the start of the breeding season. Variation in participation in breeding is typical of the hare and may be due to intrinsic factors and/or variation in climate (Marboutin et al. 2003, Smith et al. in press a).

We found a low incidence of lactation in pastural habitats, but incidence of pregnancy and litter size was similar in arable and pastural habitats. This suggests that either survival of leverets is lower in pastural than in arable areas, or females suckle

leverets for shorter periods of time, perhaps because they are in relatively poor condition, and cannot continue to produce milk. Both possibilities would result in reduced survival of leverets or juveniles. Leveret and juvenile survival has been estimated at 0.25-0.50 in an arable area (Pépin 1989), 0.23 in a mixed agricultural area and 0.18 in a mainly pastural area (Frylestam 1980b).

Body condition and dietary quality

The snapshot views of body condition provided by UN:C and SUN, and of dietary quality provided by the analysis of stomach contents, were similar in hares from arable and pastural habitats, suggesting that in both habitats hares are able to fulfil their short-term nutritional needs. Our values for the bone marrow index are similar in both habitats, and similar to those in other lagomorphs (Warren & Kirkpatrick 1978, Henke & Demarais 1990).

The difference we found in kidney fat index and body size suggests that energy expenditure is higher in pastural areas than in arable areas, perhaps due to climatic differences. Body condition is often correlated with nutritional quality and is therefore a measure of habitat quality (Villafuerte et al. 1997), but body condition in snowshoe hares improves if predators are removed as well as if diets are supplemented (Hodges, Stefan & Gillis 1999). As well as nutritional quality, foraging behaviour and predation risk determine body condition (Villafuerte et al. 1997).

We expected body condition and dietary quality to be low in pastural areas where the density of hares is relatively low. However, compared with those from arable areas, hares from pastural areas in this study were able to obtain a similar quality diet, but were unable to maintain as good body condition.

Conclusions

We present differences in demography which help to explain the differences in density of hares in arable and pastural areas. The directionality of non-significant effects was mostly as expected (see e.g. Table 3a). Our results suggest that the arable a and arable b landscape types are more similar to each other (in terms of demography and body condition of hares), and more distinct from pastural landscape types than suggested by estimates of hare density (Hutchings & Harris 1996).

Pasture is a sub-optimal habitat for hares, where energy expenditure is relatively high, body condition is relatively poor, incidence of lactation in late winter and thus recruitment is reduced, but food quality is similar to that in arable areas. Reduced survival of leverets to weaning in pastural areas, coupled with a pre-breeding age structure which is similar in arable and pastural areas, suggest that post-weaning juvenile survival is be lower in arable areas than in pastural areas. Also, adult survival may be relatively low in pastural areas, due to relatively poor body condition. Our data confirm that pastural landscape types are on average warmer than arable landscape types (Bunce et al. 1996) and experience more precipitation. Unfavourable climatic conditions are therefore associated with pastural habitats. High precipitation results in mortality in leverets (Hackländer, Arnold & Ruf 2002), and high winter temperatures result in high levels of recruitment, but also in high levels of mortality through increased transmission of disease (Hewson & Taylor 1975; Hackländer, Arnold & Ruf 2002). Pastural areas also support higher numbers of foxes than arable areas (as indicated by numbers shot; Tapper 1992).

Implications

Research into the conservation of brown hares needs to focus on determining the causes of death of wild hares. Although foxes are common in areas where hares are rare (Vaughan et al. 2003) and predator removal may help to increase the population (Lindström *et al.* 1994), the provision of permanent cover without changes in numbers of predators can also result in increased numbers of hares (Slamečka 1991).

Conservation efforts should therefore concentrate not only on the provision of year-round forage (Panek & Kamieniarz 1999, Vaughan et al. 2003) and on the inclusion of some arable land in mainly pastural habitats (Vaughan et al. 2003), but also on the reduction of predation and exposure to unfavourable weather by the provision of year-round vegetative cover (Smith et al. in press b). Suitable cover is provided by fallow land (Vaughan et al. 2003), rough grass margins (Panek & Kamieniarz 1999), and shelterbelts, woodland, and hedges (Tapper & Barnes 1986, Slamečka 1991). Efforts to conserve the hare in accordance with the Bern Convention (Anonymous 1979) or to achieve the aims of the BAP (Anonymous 1995) need to focus on increasing the survival of leverets and adult hares (Smith et al. submitted).

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Table 1. Sample sizes (numbers of adult carcasses; total=808) among landscape types and farmland types. Percentages are of total number shown; levels of variables from which <5% of hares originated are not shown.

Landscape type	Arable a	209 (27%)
	Arable b	502 (64%)
	Pastural	72 (9%)
Farmland type	Arable	676 (86%)
	Pastural	107 (14%)

Table 2. Percentages of young female hares killed in winter pregnant and/or lactating in different landscape and farmland types. Sample sizes (total number of hares for which information about reproduction is available) are shown.

Landscape type	Arable a	90% (*n*=10)
	Arable b	62% (*n*=21)
	Pastural	100% (*n*=1)
Farmland type	Arable	75% (*n*=28)
	Pastural	29% (*n*=7)

Table 3. Percentages of adult females (a) pregnant and (b) lactating in late winter. Sample sizes (numbers for which data on pregnancy or lactation are available) are shown. Overall in late winter, 41 adult females were both pregnant and lactating.

(a) Pregnant		
Landscape type	Arable a	69% (*n*=89)
	Arable b	63% (*n*=207)
	Pastural	40% (*n*=10)
Farmland type	Arable	65% (*n*=279)
	Pastural	53% (*n*=19)
(b) Lactating		
Landscape type	Arable a	62% (*n*=50)
	Arable b	27% (*n*=146)
	Pastural	13% (*n*=8)
Farmland type	Arable	37% (*n*=182)
	Pastural	0% (*n*=15)

Table 4. Descriptive statistics of body condition, size, and weight variables for adult hares killed in winter.

	Males		**Females**	
	Mean (min-max)	***n***	**Mean (min-max)**	***n***
UN:C	29.2 (3.6-162.0)	202	19.2 (3.3-53.7)	70
SUN	32.8 (7.8-70.0)	111	29.7 (2.8-84.3)	112
Kidney fat score	3.0 (0-7)	348	4.1 (0-8)	329
Bone marrow fat index	47.0 (33.9-61.8)	40	43.5 (17.4-61.2)	49
Hind foot length (cm)	14.4 (12.1-15.7)	352	14.5 (12.4-15.7)	332
Cleaned weight (kg)	2.6 (1.4-3.4)	350	2.9 (1.4-3.8)	330
Body weight (kg)	3.2 (2.0-4.1)	349	3.6 (1.8-4.6)	331

Table 5. Final binary or nominal logistic regression models of body condition variables on dependent variables landscape type and farmland type. Only variables which were significant at the simple level were included in the final model. Variables which were significant at the simple level but not in the final model are shown. In all cases the directionality of simple effects was as expected, i.e. hares from high density areas were in better condition than those from low density areas. In final models, the reference event is always the level with the lower hare density, so a positive coefficient indicates an effect as expected. For males, no variable was significant for farmland type. Log-likelihood tests and goodness-of-fit tests are shown for the final models. Odds ratios are the odds of change in the dependent variable from the reference event for a one-step increase in the independent variable; CI=confidence intervals; fat score = kidney fat score; HFL= hind foot length (cm); CW=cleaned weight (kg); Aa=arable a, Ab=arable b, P=pastural landscape types; A=arable, P=pastural farmland types.

Dep. variable, gender	Indep. var.	Levels of dependent variables	Coeff. ± standard error	Z, *P*	Odds ratio (95% CI)	Var. sign. at simple level
Landscape	CW	Aa vs. P (ref event)	1.64±0.98	1.7, 0.094	5.1(0.8-34.9)	fat score, HFL
Males	CW	Ab vs. P (ref event)	2.40±0.98	2.4, 0.015	11.0(1.6-75.2)	
Δd_6=25.6, *P*=0.000 Deviance goodness-of-fit *P*=1.00						
Landscape	CW	Aa vs. P (ref event)	2.54±1.26	2.0, 0.043	12.7(1.1-149.0)	fat score, HFL
Females	CW	Ab vs. P (ref event)	2.67±1.23	2.2, 0.030	14.4(1.3-159.2)	
Δd_6=26.6, *P*=0.000 Deviance goodness-of-fit *P*=1.00						
Farmland	CW	A vs. P (ref event)	1.26±0.62	2.1, 0.040	3.5(1.1-11.8)	-
Females	Δd_1=4.0, *P*=0.045 Deviance goodness-of-fit *P*=0.99					

Table 6. Repeated-measures ANOVAs on body condition and size parameters for within-pair factor: habitat (arable and pastural) and between-pair factor: gender. Source = source of variation, df = degrees of freedom, MS = mean square, x =interaction term.

Parameter	Source	df	MS	F	*P*
Kidney fat score	habitat	1	29.58	8.79	0.004
	habitat x gender	1	3.73	1.11	0.296
	error (habitat)	61	3.36		
	gender	1	14.48	3.10	0.083
	error (gender)	61	4.67		
Bone marrow fat index	habitat	1	91.67	1.40	0.245
	habitat x gender	1	34.08	0.52	0.475
	error (habitat)	31	65.29		
	gender	1	353.50	2.54	0.121
	error (gender)	31	138.99		
Hind foot length (cm)	habitat	1	1.93	5.71	0.019
	habitat x gender	1	0.03	0.08	0.776
	error (habitat)	73	0.34		
	gender	1	0.29	0.66	0.420
	error (gender)	73	0.45		
Cleaned weight (kg)	habitat	1	142.03	4.54	0.037
(Box-Cox transformed;	habitat x gender	1	0.07	0.00	0.960
lambda = 2.697)	error (habitat)	61	31.28		
	gender	1	86.98	3.15	0.081
	error (gender)	61	27.60		

Table 7. Descriptive statistics of dietary quality of paired hares. Only pairs in which the variable could be measured in both hares are included.

		Males		**Females**	
		Mean (min-max)	***n***	**Mean (min-max)**	***n***
% ash	Arable	14.6 (8.2-28.8)	18	16.4 (3.0-46.9)	22
	Pastural	9.3 (4.9-17.7)	18	11.5 (4.7-37.6)	22
% protein	Arable	32.8 (17.1-44.0)	18	28.9 (15.3-38.7)	22
	Pastural	32.8 (26.1-50.3)	18	28.6 (20.6-35.3)	22
% fat	Arable	6.1 (3.0-10.4)	18	5.8 (1.7-8.7)	22
	Pastural	6.0 (4.4-8.8)	18	6.0 (1.7-8.7)	22
% fibre	Arable	14.4 (10.4-22.6)	18	19.2 (10.7-27.5)	22
	Pastural	17.7 (4.8-28.1)	18	22.2 (11.9-26.1)	22
% carbohydrates	Arable	32.2 (22.3-54.9)	18	29.7 (10.3-46.1)	22
	Pastural	34.2 (30.5-39.1)	18	33.7 (20.8-42.6)	22
Total dry weight (g)	Arable	9.4 (5.0-16.9)	15	10.2 (4.3-21.8)	17
	Pastural	10.2 (5.1-19.0)	15	9.5 (5.6-14.7)	17
Total energy (kJ)	Arable	121.6 (61.2-193.6)	15	122.4 (46.1-259.8)	17
	Pastural	139.1 (70.4-276.9)	15	120.1 (75.4-191.8)	17

Table 8. Repeated-measures ANOVAs on dietary quality parameters for within-pair factor: habitat (arable and pastural) and between-pair factor: gender. Source = source of variation, df = degrees of freedom, MS = mean square, x =interaction term.

Parameter	**Source**	**df**	**MS**	**F**	***P***
Log (% ash+1)	habitat	1	0.48	9.82	0.003
	habitat x gender	1	0.00	0.04	0.852
	error (habitat)	38	0.05		
	gender	1	0.02	0.62	0.435
	error (gender)	38	0.03		
% protein	habitat	1	0.42	0.03	0.870
	habitat x gender	1	0.55	0.04	0.852
	error (habitat)	38	15.41		
	gender	1	318.74	5.99	0.019
	error (gender)	38	53.19		
% fat	habitat	1	0.09	0.04	0.851
	habitat x gender	1	0.58	0.24	0.629
	error (habitat)	38	2.44		
	gender	1	0.45	0.17	0.686
	error (gender)	38	2.68		
% fibre	habitat	1	92.23	6.73	0.013
	habitat x gender	1	25.31	1.85	0.182
	error (habitat)	38	13.71		
	gender	1	262.38	11.20	0.002
	error (gender)	38	23.43		

% carbohydrate	habitat	1	184.07	4.92	0.033
	habitat x gender	1	19.59	0.52	0.474
	error (habitat)	38	37.44		
	gender	1	43.44	1.04	0.315
	error (gender)	38	41.96		
Total dry weight (g)	habitat	1	0.01	0.00	0.980
	habitat x gender	1	8.75	0.77	0.388
	error (habitat)	30	11.43		
	gender	1	0.16	0.01	0.922
	error (gender)	30	16.33		
Total energy (kJ)	habitat	1	927.76	0.46	0.503
	habitat x gender	1	1563.61	0.78	0.386
	error (habitat)	30	2016.52		
	gender	1	1329.51	0.45	0.506
	error (gender)	30	2938.17		

Figure legend

Figure 1. Map of England and Wales showing the regions and the 125 locations from each of which 1-57 hares were included in the analysis (○).

Figure 1